BIOLOGICAL EVALUATION OF THE ASSOCIATIONS BETWEEN ANIMAL SIZE, FEEDING BEHAVIOR, BLOOD METABOLITES AND FEED EFFICIENCY IN BEEF CATTLE

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ABSTRACT

The biological variation in feed efficiency is regulated by multiple physiological mechanisms relevant to energy use in livestock species. The current study examined the associations between body composition, feeding behavior, linear body measurements and plasma metabolites with different measures of feed efficiency in growing heifers, finishing steers and mature pregnant cows. Our findings indicate that inclusion of body size measurements in prediction models of gain and intake improved the models' accuracy and might account important differences related to eating capacity. Among the traits evaluated, feeding behavior possessed stronger associations with efficiency measures and displayed differences between efficient and inefficient animals. The associations between the traits studied herein varied across the efficiency measures used and beef cattle stage of production. Thus, selection criteria and performance evaluation based on efficiency measures should account for these traits, combined with animal's stage of production and system's outputs of interest.

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LIST OF ABBREVIATIONS

°C .....Degree Celsius

ADF .....Acid detergent fiber

ADG .....Average daily gain

ADGrbw .....Average daily gain relative to body weight

BIC .....Bayesian information criterion

BKFT .....Backfat thickness

BW .....Body weight

$BW^{0.75}$ .....Metabolic body weight

Ca .....Calcium

CCE_{d21} .....Cow/calf efficiency at day 21

cm .....Centimeter

cm^2 .....Centimeter square

CP .....Crude protein

CSB .....Concentrated separator by-product

CV .....Coefficient of variation

d .....Days

DDGS .....Dried distiller's grains with solubles

DM .....Dry matter

DMI .....Dry matter intake

DMIrbw .....Dry matter intake relative to body weight

F:G .....Feed to gain ratio

FCR .....Feed conversion ratio

g .....g-force

g .....Grams

G:F .....Gain to feed ratio

GIT .....Gastrointestinal tract

h .....Hour

ID .....Identification

iFG .....Initial flank girth

iHG .....Initial heart girth

iHW .....Initial hip width

iMG .....Initial mid-girth

IU .....International units

Kg .....Kilogram

KPH .....Kidney pelvic heart fat

LCFA .....Long-chain fatty acids

m .....Meters

ME .....Metabolizable energy

mIMFT .....Mid-point intramuscular fat

min .....Minutes

mL .....Milliliter

mm .....Millimeter

mmBW .....Mid-point metabolic body weight

mmpcBW .....Mid-point pregnancy corrected metabolic body weight

mpcmBW .....Mid-point pregnancy corrected body weight

mRBEA .....Mid-point ribeye area

mRBFT .....Mid-point ribfat

mRUMP .....Mid-point rump fat

N .....Nitrogen

NDF .....Neutral detergent fiber

NEFA .....Non-esterified fatty acid

P .....Phosphorus

pcADG .....Pregnancy corrected average daily gain

pcADGrbw .....Pregnancy corrected average daily gain in relation to body weight

pcBW .....Pregnancy corrected body weight

pcDMIrbw .....Dry matter intake in relation to pregnancy corrected body weight

pregd .....Gestation length

PUN .....Plasma urea nitrogen

R MSE .....Root mean square error

R^2 .....Coefficient of determination

RBEA .....Ribeye area

RFI .....Residual feed intake

RFI_{Koch} .....Residual feed intake Koch model

RFI_{size} .....Residual feed intake size adjusted model

RFI_{us} .....Residual feed intake ultrasound adjusted model

RG .....Residual gain

RG_{Koch} .....Residual gain Koch model

RG_{size} .....Residual gain size adjusted model

RG_{us} .....Residual gain ultrasound adjusted model

SAS .....Statistical analysis system

SEM .....Standard error of the mean

TG ..... Triglycerides

TMR .....Total mixed ration

1. INTRODUCTION AND LITERATURE REVIEW

1.1. Introduction

The origin of cattle in North America is generally linked to Christopher Columbus' second expedition in the 15th century. For the first 400 years that cattle were in the continent, herd size was relatively small and feeding practices relied solely on grazing of natural forages, while the animals were primarily used for milk and work-force (Corah, 2008). However, with the development of the regions in the United States territory, as reviewed by Ball (1998), approaches started to change in a feeding management perspective. Hence, the earliest mention of corn feeding and cattle "fattening" in historical proceedings appeared later in the 19th century (reviewed in Corah, 2008). Undoubtedly, the first steps of the beef cattle sector were not shaped into the current modern agricultural system, which among others involves maximizing reproductive and productive efficiencies, finishing animals with a grain-based diet and shortening the production cycle, until the middle of the 20th century. By that time, researchers started to investigate the effects of grain-based finishing diets and quickly realized the positive effects of feeding an increased proportion of grains, more specifically corn, into final body weights, average daily gain (ADG) and improved carcass quality (reviewed in Corah, 2008).

The current model of beef production in the United States is a highly specialized system that is diversified with various types of operations, which enables different possible paths to be taken between calving and slaughter. The beef cycle starts with the cow-calf producer, who maintains a breeding herd of cows typically maintained on pasture and/or fed forages year round. Calves are weaned at 6 to 10 months of age, when weighing on average between 200 to 300 kg. The calves weaned have multiple production routes that can be followed and combined differently: 1) calves may be sent to a backgrounder or stocker, who will continue to graze them until they are

12 to 16 months old; 2) calves may be sold at an auction market; or 3) in the case of heifer calves, they may also be kept by the cow-calf producer who wishes to use them as replacement for the cow herd; 4) some calves do not go through the auction market and can go to the feedlot (finishing phase) straight from the cow-calf producer, or the backgrounder/stocker. Thus, the feedlot phase can last from an average of 4 to 6 months, and by the end of it, market weights are typically between 550 to 630 kg (North American Meat Institute, 2014).

Furthermore, cattle production is one of the most important industries in the United States. In 2015, the Economic Research Service (ERS) reported that this segment of the agricultural sector accounted for $78.2 billion dollars in cash receipts and was the largest cash receipt forecasted, representing 21% of the profits from agricultural commodities (USDA, 2016). It is interesting to note that with the advance of the beef cattle industry, and taking into account the importance of this sector to the overall economics of the United States, there was also a concomitant development of the commercial cattle feeding industry. Indeed, this industry also represents a substantial portion in the context of agricultural commodities. In 2015, corn production yielded 12% of total cash receipts and was the second largest cash receipt in the agricultural sector (USDA, 2016). Therefore, it is sensible to recognize the importance to consider those two segments of agricultural production together when establishing beef cattle management strategies to maximize production and overall profits. Especially when taking into account that feed is a major expense in all livestock production systems, and accounting for up to 70% of production costs in beef cattle enterprises (Herd et al., 1998). Certainly, the future of the beef industry, as wisely concluded by Corah (2008): "*will be dependent on our ability to continue producing high-quality beef for a global market through effective use of genetics, new technologies, and economic management strategies*".

1.2. Feed efficiency and the beef industry

Even though beef production in the United States is a highly diversified sector with multiple segments, the division of this industry can be roughly divided into two production sectors: cow-calf operations and feedlot cattle feeding. Regardless of stage of production, the provision of feed constitutes the largest expense to agricultural production systems. It should be noted, however, that the cow-calf herd might account for 65 to 85% of overall feed costs in the production system (Montaño-Bermudez et al., 1990). This relationship becomes even more important when considering feedlot cattle, because the high cost of feeding means that profitability depends on the efficient and productive use of feed for maintenance and growth with minimal excesses and losses (Nkrumah et al., 2006). In fact, feed efficiency becomes the most important factor that a feedlot can control to gain an advantage over the competition (Lee, 1993).

Additionally, livestock production systems are one of the largest users of agricultural lands (Thornton, 2010). Thus, there are relevant environmental implications associated with this production system. The statistical estimation and reports of the contribution of livestock production to global greenhouse gas emissions can often vary, but the FAO (2006) estimated that livestock production contributed 18% of all emissions. With the expectations of an increase in the world population, and consequently a higher demand for animal products, there are also reports suggesting that growth in the livestock sector may contribute to increases in greenhouse gas concentrations in the atmosphere (FAO, 2013) through the waste product of animals.

Therefore, optimizing the production of animal products in relation to the amount of feedstuffs fed to animals would bring significant economic (Arthur and Herd, 2005) and environmental (Nkrumah et al., 2006) benefits to the livestock sector. Taking into account the economic interest in feed efficiency, this trait has been a hot topic and a tremendous focus of

attention for producers, researchers and companies in the agriculture business within the past few years. There are several factors that can influence feed efficiency including age, sex, type of diet, breed, production level, environmental temperature, the use of growth promotants, physical activity, and many other management and environmental variables (NRC, 2016). The improvement of cattle feed efficiency can be accomplished through management practices and decisions, that can vary from: handling practices (Grandin, 1998); housing facilities and environmental conditions (Grandin, 2016) to dietary manipulation with the incorporation of feed additives in the diets and anabolic implants (Song and Choi, 2001); as well as genetic selection for improved efficiency (Arthur and Herd, 2005), which may often rely on measures of feed efficiency.

1.3. Feed additives and feed efficiency

The use of feed additives, such as ionophores, can improve feed efficiency and body weight gain by altering rumen fermentation patterns. These compounds disrupt the ion concentration gradient across microorganisms' membranes, causing them to enter a futile ion cycle. Briefly, the disruption of the ion concentration prevents the microorganism from maintaining normal metabolism and causes the microorganism to expend extra energy. Therefore, these compounds function by selecting against or negatively affecting the metabolism of many gram-positive rumen bacteria (i.e., *Ruminococcus albus, R. flavefaciens, Eubacterium ruminantium*) and protozoa that proposedly decrease efficiency of digestion in the rumen. By controlling certain protozoa and bacteria in the rumen, less methane is generated (Guan et al., 2006) and ruminal protein breakdown is decreased, which results in decreased ammonia production. The shift in ruminal bacteria population and metabolism allows more efficient bacteria to benefit through an increase in the

amount of propionic acid and a decrease in the production of acetic acid and lactic acid. Therefore, cattle experience an increase in the overall energy status and use feed resources more efficiently.

Certain β-adrenoreceptor agonists (β-agonists) are also labeled for use as feed additives in food-producing animals in the United States to improve feed efficiency, increase growth rate, alter adipose accretion, and increase muscle mass (Johnson and Chung, 2007). In a simplified manner, their mode of action is to bind to receptors on adipocytes, redirect the metabolism of fat and reduce fat deposition. Consequently, less fat is produced and less fat is stored in the carcass. The compounds bind to receptors on muscle cells, redirect, and increase the size of muscle fibers. Muscle fiber size replaces some of the weight normally found from fat and the total carcass contains a higher percentage lean muscle. These actions reduce the energy supplied by the feed to produce weight gain. With more weight produced by the same level of feed intake, feed efficiency is improved (Johnson et al., 2014).

Despite the addition of additives or implants into finishing strategies as ways to improve feed efficiency and maximize outputs, the selection for animals with enhanced metabolic efficiencies, which is based on the known biological variation between animals (Johnson et al., 2003), also emerges as a viable option to improve feed efficiency. As proposed by Archer et al. (1999), this improvement in efficiency of energy and feed use in cattle could be achieved using many different measures of feed efficiency.

1.4. Diet types and feed efficiency

There are several factors known to contribute, influence and that might potentially shift how nutrients are used in cattle; a couple of examples are the different breed types (Schenkel et al., 2004), sex (Elzo et al., 2009; Nkrumah et al., 2004), age (Carstens et al., 1989), physiological stage (Johnson et al., 1990), and production level (NRC, 2016). Furthermore, another relevant

point is the dietary treatment of the animals. It is important to note that the relationship between diet types (i.e., forage-based, concentrate-based), digestibility and feed efficiency is not well characterized in cattle (Russell et al., 2016) and might bring significant differences to efficiency of nutrient utilization. In fact, it is suggested that animals may perform differently depending on the diet provided (Goonewardene et al., 2004).

For instance, Meyer et al. (2008), while evaluating females on a concentrate diet found significant differences related to feed efficiency phenotypes, measured through residual feed intake (RFI), but no differences were found when the cows were re-evaluated on a pasture-based system. Moreover, Fan et al. (1995), when evaluating bulls on concentrate vs. roughage diets, found that bulls fed a higher roughage diet had a negative RFI when compared to bulls fed a more concentrate diet. Overall, the lack of standard diet not only represents a concern when evaluating animals, but also a limitation for comparison across studies that should be carefully taken into account prior to any feed efficiency evaluation.

1.5. Measures of feed efficiency

Efficiency of feed utilization can be assessed through a myriad of different measurements (Swanson and Miller, 2008). Nevertheless, one of the key factors regulating the outcome of most of the research involving feed efficiency is the definition of the term feed efficiency (Freetly, 2014). Different methods will most likely have different outcomes, which could be advantageous or disadvantageous, depending on the portion of the beef cycle. As reviewed by Swanson and Miller (2008), it can be challenging to define specific biological or economic inputs and outputs. Thus, care must be taken in how these values are interpreted and used in developing nutrition or animal breeding programs. Additionally, there are some practical limitations to determining any measure of feed efficiency, since the assessment can be highly laborious, time consuming (Herd

et al., 2003), and can be an expensive method if taking into account the equipment and labor needed (Moore et al., 2009). Regardless of the efficiency measure, the biological basis associated with the variation in efficiency of feed utilization has not been completely elucidated in livestock species. A better understanding of the biological basis associated with feed efficiency might result in the improvement of the prediction of correlated responses to selection, the identification of traits that are less expensive to measure in comparison to feed intake and efficiency, and finally, it might suggest alternative, non-genetic methods, which might be useful tools to manipulate metabolism in beef cattle (Montanholi, 2007; Swanson and Miller, 2008).

1.5.1. Gross efficiency

Gross efficiency is one of the most broadly used measure of feed efficiency and is highly used in feedlot operations. This measure can simply be calculated through the ratio of dry matter intake (DMI) to live weight gain (gain to feed, G:F) or its inverse (feed conversion ratio, FCR or F:G) over a defined period of growth (Archer et al., 1999; Swanson and Miller, 2008). Therefore, a more feed efficient animal would have higher G:F ratio value, which would indicate more gain per unit of required feed. Gross efficiency is a satisfactory index for monitoring feedlot cattle performance and is widely used in the beef industry (Schenkel et al., 2004). However, even though selection for improved gross efficiency may improve performance during growing and finishing phases of beef cattle production, it may not necessarily improve the profitability of the entire production system (Arthur et al., 2001). It has been suggested that this measure may have detrimental effects on overall cow efficiency when used as a selection tool for the herd (Archer et al., 1999). This is mostly related to the fact that selecting for improved gross efficiency may result in an increase in genetic merit for growth, leading to an increased mature cow size, which could ultimately increase feed costs for the cow herd (Swanson and Miller, 2008).

1.5.2. Residual gain

Residual gain (RG) is an alternative measurement to quantify efficiency of feed utilization and has been proposed to be used in beef cattle by Koch et al. (1963). This measure is defined and calculated by the difference between actual gain (i.e. average daily gain, ADG) and the predicted gain, which is performed through regression analysis within the test population, taking into account animals' body weight (i.e. estimation of background energy requirements), feed intake (Koch et al., 1963) and body composition (Freetly, 2014). Thus, a feed efficient animal would have a higher RG value, as it gained more live body weight than what it was predicted for its weight, intake and carcass composition. However, similarly to the gross efficiency approach, this measure can be highly correlated to growth (Crowley et al., 2010).

1.5.3. Residual feed intake

Residual feed intake represents the difference between average feed intake and expected feed intake, as estimated by an animal's background energy requirements (Koch et al., 1963). Most studies have calculated expected feed intake by regression of actual feed intake on metabolic body weight, ADG (Koch et al., 1963), and carcass characteristics (Montanholi et al., 2009). From this difference, an animal with a low RFI is considered to be feed efficient, as it ate less than their counterparts eat, but still produced the same outputs. Some of the benefits are that RFI is phenotypically independent of the production traits used in the calculation, relatively repeatable, with a moderate heritability (Swanson and Miller, 2008). These characteristics that altogether, suggest that RFI has the ability to be used in selection programs (Crowley et al., 2011). Therefore, this measure has gained increased usage in research and to some level, application by the beef industry (i.e. USDA Feed Efficiency Project, United States; The 2014 LSARP project, Canada; Australian Angus Association, Australia).

Additionally, since RFI is considered not to be highly correlated to the level of production (Richardson et al., 2001), it might also represent an interesting trait for studying the biological factors associated with feed efficiency. Within the past two decades, studies with the objective of understanding the underlying mechanisms of feed efficiency through RFI are abundant. A few examples of biological processes related to RFI that may contribute to the indirect assessment of RFI include: measurement of heart rate (Munro et al., 2017), stress responses (Montanholi et al., 2010; Munro et al., 2017) hepatic and small intestinal micro-architecture (Montanholi et al., 2013; Montanholi et al., 2017) and metabolic profile of blood (Gonano et al., 2014; Montanholi et al., 2017).

1.5.4. Cow/calf efficiency

Cow/calf efficiency has been used as an approach to examine efficiency of beef production (Jenkins and Ferrell, 1994). This measure is proposed to be a better measure of production system efficiency than the other measures of biological efficiency and is thought to be an useful indicator to verify the phenotypic variation in the beef herd (Archer et al., 1999). The calculation of this measure involves measuring the total feed intake, both for the dam and the progeny, over an entire production cycle from weaning of one calf to the weaning of another calf (Jenkins and Ferrell, 1994). This measure is expressed in relation to the weight of the calf weaned to express the efficiency of the cow/calf unit. As reviewed by Archer et al. (1999) and Swanson and Miller (2008), there are problems associated with this measure, which include the fact that the intake of the progeny is only measured until the weaning period, leaving a lack of information regarding the performance from weaning until slaughter or if the animals are to be used as replacements in the cow herd, the genetic merit from the sire to both cow and calf, as well as huge limitations from a

practical standpoint requiring considerable cost and labor to evaluate these parameters for an extended time period.

1.6. Metabolic aspects of feed efficiency

The biological processes involved in maintenance and growth are energetically divergent and are dependent on the metabolic demand (Kleiber, 1961) and physiological stage of an animal (NRC, 2016). Basal metabolism is defined as *"the result of chemical change that occurs in the cells of an animal in the fasting and resting state using just enough energy to maintain vital cellular activity, respiration, and circulation"* (NRC, 1981). Such tasks require constant energy even when the organism is at a resting stage (Brody, 1945). The successful meeting of maintenance requirements is only viable with energy that comes from dietary intake. Consequently, imbalances between energy use and need are a marked cause of weight gain, when there is exceeding energy for maintenance that can be devoted to growth processes; or weight loss, when there is not enough energy provided for maintenance, forcing the body to use its energy reserves (i.e., muscle and fat) to provide the proper functioning of vital functions.

Metabolizable energy (ME) becomes a very important concept in the overall understanding of the metabolic aspect of feed efficiency, since ME is the portion of food energy which is available for metabolic processes in a living animal (Armsby, 1917). This can be understood as the subtraction of energy losses (i.e., feces, urine, and gaseous products of digestion) from the total gross energy (Baldwin et al., 1980). Furthermore, ME supplied to the animals at a maintenance level can be divided into net energy for maintenance, which will be the energy available for function of vital organs in the body, and heat increment for maintenance, which will be the energy associated with expenditures from digestion and assimilation processes (Baldwin et al., 1980). Furthermore, the maintenance requirements can be divided into two major groups: the first, service

functions, which are responsible for respiration, functioning of the heart, lungs, kidney, liver, and other vital organs, as well as removal of wastes. Energetically, this accounts for 36 to 50% of total basal energy expenditure; and the second, cellular maintenance functions, that can be further divided into protein turnover, lipid turnover, and ion transport. This represents the remaining 40 to 56% of basal energy requirements (Baldwin et al., 1980). Noteworthy, there are studies that suggest the partition of energy towards maintenance and production can vary greatly among animals because of individual variation in relation to maintenance requirements (Johnson et al., 2003), as well as physiological stage (Johnson et al., 1990). Moreover, one of the possible explanations for the basis of the biological differences regarding efficiency of energy use in beef cattle is the assumption that feed efficient animals might potentially have lower energy requirements for maintenance requirements (Herd and Arthur, 2009).

1.7. Potential sources of variation in feed efficiency

Discovering the traits that are responsible for phenotypic differences in efficiency of feed utilization could lead not only to the identification of indirect markers of feed efficiency, but also aid in the understanding of the biological basis of this phenomenon. Historically, the study of feed efficiency traits has suggested that there is not a single mechanism controlling the phenotypic differences in feed efficiency (Oddy, 1999), and because most feed efficiency traits are correlated with production traits (i.e., growth; Archer et al., 1999), it has been difficult to investigate the physiological mechanisms underlying this variation.

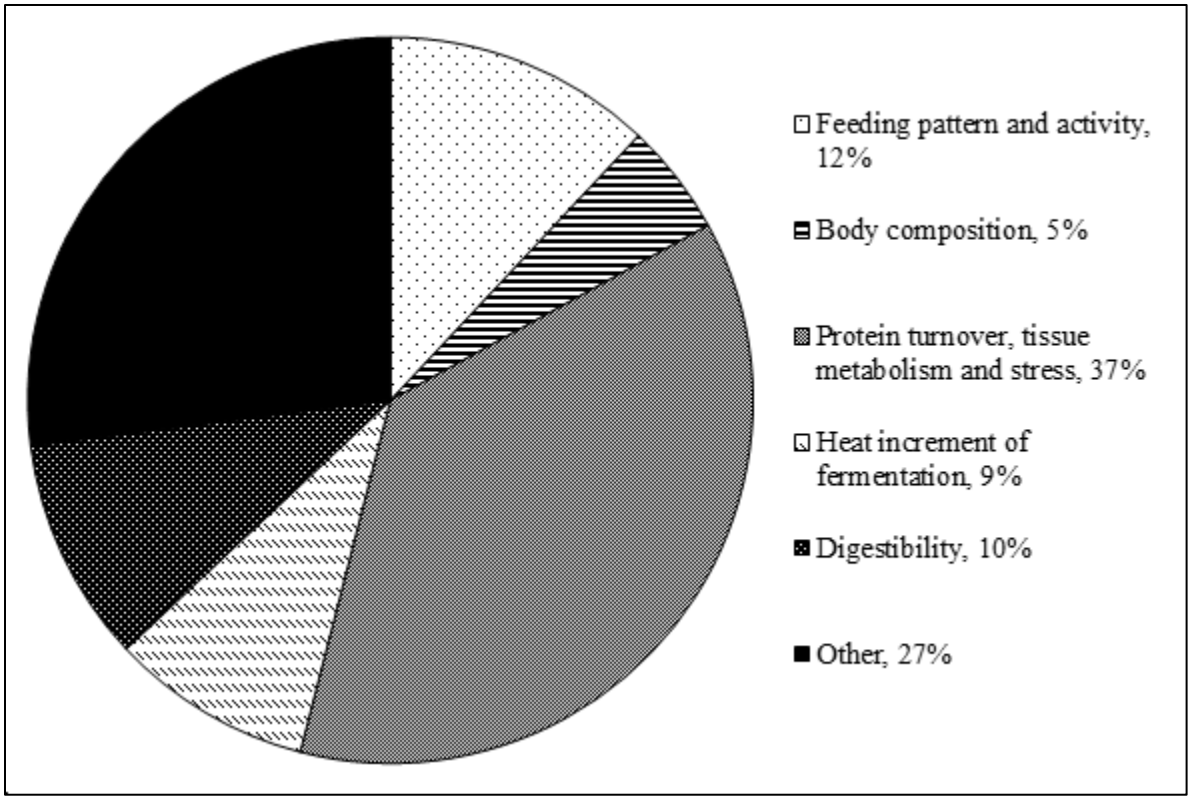

Figure 1.1. Physiological mechanisms proposed to contribute in the biological variations of feed efficiency, measured through RFI. Adapted from Richardson and Herd (2004).

Richardson and Herd (2004), while summarizing a series of experiments in beef cattle divergently selected for RFI, proposed that 73% of the variation of feed efficiency, measured through RFI, could be explained by processes involving animal feeding patterns and activity, body composition, heat associated with metabolic processes, digestibility and protein turnover, tissue metabolism and stress (Figure 1.1). Notably, there are a large number of processes that could be contributing to the variation in feed efficiency. However, the following topics reviewed within this Chapter will focus on traits that are emphasized and measured in the experiments conducted for this thesis (Chapters 2 and 3).

1.7.1. Animal size

It is well known that body size, in mature and growing phases, has both biological and economic effects on the efficiency of animal production (Dickerson, 1978). In fact, much research

has been conducted to investigate and potentially determine what the optimal animal size is to achieve maximum biological or economic efficiency (Johnson et al., 2010). Despite the fact that feed intake can be highly influenced by animal size (NRC, 1987), linear measurements of body dimensions may also provide insight into changes in maintenance energy requirements and surface area and gut capacity (Kleiber, 1961). Additionally, measures of the animal's girth have been shown to have strong correlations with body weight variation (Heinrichs et al., 1992), since these measurements (i.e. heart girth and mid-girth) can be greatly influenced by gastrointestinal tract fill (Wood et al., 2014).

Wood et al. (2014) found, that in mature pregnant cows, hip width and body length were positively correlated with dry matter intake and mid-point body weight. Moreover, RFI was negatively correlated with body length, while G:F was negatively correlated with heart girth, mid-girth, and flank girth. It is interesting to note that Basarab et al. (2003), Kelly et al. (2010), and Wood et al. (2014) did not find differences regarding animal height (i.e. hip height) across different RFI phenotypes in growing animals. This is suggestive that, in the context of feed efficiency, relevant body measurements are associated with areas that reflect internal organ fill and capacity, such as measurements of girth.

In the current scenario of feed efficiency research, differences in gross measurements of animal size (i.e. linear body measurements) are not being emphasized even though previous studies suggest that linear measurements may be associated with the different efficiency phenotypes (Wood, 2013). Although it becomes very clear that the biological basis of feed efficiency is more complex than animal size and dimensions (Herd et al., 2004), the evaluation of these parameters might assist in the understanding of the biological variation associated with efficiency of feed

utilization. Thus, body measurements might not only aid in identifying superior phenotypes, but might also aid in the enhancement of gain and intake prediction models.

1.7.2. Feeding behavior

Animal behavioral responses can alter physical activity and thus influence total energy expenditure and feed efficiency (Susenbeth et al., 1998). In fact, according to Richardson and Herd (2004), feeding patterns and activity could account for up to 12% of the variation in RFI (Figure 1.1). Many studies indicate distinguished behavioral patterns across cattle with differing feed efficiency (Nkrumah et al., 2006; Nkrumah et al., 2007; Kelly et al., 2010; Montanholi et al., 2010). Generally, it has been shown that more feed efficient (low-RFI) cattle typically engage in less daily feeding activity (Golden et al., 2008), eat smaller meals (Montanholi et al., 2010) at a slower pace (Kelly et al., 2010), and visit the feeder less often (Kelly et al., 2010; Montanholi et al., 2010) during the feeding test. Moreover, studies also show that more feed efficient animals typically engage in 22% fewer daily feeding events compared with less efficient animals (Nkrumah et al., 2006; Nkrumah et al., 2007; Kelly et al., 2010). Moreover, it is suggested that feed efficient cattle prefer to eat at the time fresh feed is offered (King et al., 2016). The use of pedometers has also indicated that feed efficient cattle spend more time ruminating than feed inefficient cattle (Herd, 2009).

This evidence indicates the possibility of optimizing the screening for feed efficiency by including feeding and social behavior traits into selection tools and/or management strategies. Thus, the evaluation of feeding behavior in the context of feed efficiency may not only constitute another possibility to identify superior feed efficient phenotypes, but also become a trait that potentially could be used to indirectly assess feed efficiency.

1.7.3. Metabolic markers of efficiency

The biological basis associated with feed efficiency in beef cattle, reported mostly through the measurement of RFI, have been intensively investigated over the last few years. Moreover, much attention has been given to plasma analytes (i.e. metabolic hormones, enzymes and metabolites, mediators of nutrient uptake, inhibitors of tissue catabolism) that are associated with energetically demanding functions of the whole body or organ systems and that might reflect the differences in efficiency of feed utilization (Blaxter, 1962). Therefore, a myriad of analytes have been examined to identify potential physiological markers for feed efficiency, while also improving the understanding of the metabolic basis of efficiency of feed utilization in cattle (Basarab et al., 2003; Nkrumah et al., 2007; Kelly et al., 2010; Gonano et al., 2014). Metabolites such as glucose, urea and non-esterified fatty acids (NEFA), which are respectively involved in carbohydrate, protein and lipid metabolism, might reveal basic aspects of the biological differences in feed efficiency, since their concentrations are highly dependent on level of dry matter intake (Yambayamba et al., 1996), diet composition and productive priorities of the animal (Huntington, 1986), which are important players when considering the energetic basis of efficiency of feed utilization.

1.7.3.1. Plasma urea-N

Over the years, attention has been given to urea-N, which is the end-product of nitrogen metabolism in ruminants and its potential to explain and reflect some of the variation in feed efficiency. Notably, plasma urea-N (PUN) could be associated with skeletal muscle mass (Herd et al., 2004), rate of protein turnover and differences in body composition, as well as nutrient and energy losses (Swanson and Miller, 2008).

It is important to understand that, in ruminants, the movements of nitrogen across the gut can be more than double its intake (Lapierre and Lobley, 2001) and the process of nitrogen recycling, through urea, can have major metabolic expenses (Egan et al., 1984). Furthermore, one of the possible ways to analyze the importance of PUN is to focus on the recycling process of urea. Briefly, hepatic urea-N synthesis has the fates of 1) excretion in the urine, or 2) recycling back to the gastrointestinal tract (GIT) via salivary secretions or by the direct transfer across the epithelial tissues of the digestive tract (Reynolds and Kristensen, 2008). It is also known that energy expenditure by the liver increases after eating or with a sustained increase in energy intake (Huntington and McBride, 1987). Increases in activity of substrate cycles (i.e. ureagenesis, gluconeogenesis) are dependent on the level of intake (Sarraseca et al., 1998) and may be responsible for increases in energy expenditure by the ruminant GIT (Webster et al., 1975). Notably, urea synthesis is reported to account for 25% of energy expenditure in the liver (Huntington and Reynolds, 1987). Since urea is not used by the portal-drained viscera, clearing urea from the blood is also energetically demanding, but it allows another opportunity for ruminants to salvage the nitrogen in urea through bacterial urease and formation of other nitrogenous compounds (Huntington and McBride, 1987). In this context, it is sensible to hypothesize that energetically, it may be more efficient to use nitrogen from the first pass through the GIT rather than recycle and transport it in the form of urea. However, the extent of this energy expenditure also tends to vary with the physiological state of the animal. Thus, the magnitude of urea-N recycling to the GIT and its utilization for anabolic purposes is regulated by several dietary and ruminal factors, and perhaps by biological factors influencing feed efficiency.

Several researchers have reported different outcomes on studies regarding PUN studying the association between PUN and feed efficiency. Richardson et al. (2004) reported that feed

efficient steers tended to have lower concentrations of PUN in the weaning phase, but when the same steers approached the finishing phase, a higher concentration of PUN was associated with improved feed efficiency. Gonano et al. (2014), when studying the circadian profile of various plasma analytes in beef heifers at different stages (i.e. pregnant, non-pregnant), found that more efficient pregnant heifers had lower levels of PUN in late gestation. Thus, future studies are warranted to further investigate the association between PUN concentrations and feed efficiency.

1.7.3.2. Non-esterified fatty acids

Lipid metabolism is a dynamic and critically important function in both growing and mature ruminants, and has been the focus of numerous reviews (Bell, 1980; Chilliard, 1993). Briefly, lipids, such as triglycerides, from dietary supply are converted into free, non-esterified and long-chain fatty acids (LCFA) in the rumen, being mostly absorbed in the small intestine. To supply energy to peripheral tissues, the major metabolic pathway in the small intestine is to repackage LCFA into triglycerides (TG). In the peripheral tissues (mostly adipose tissue, skeletal muscle, and heart), the lipoprotein lipase enzyme is responsible for converting TG into non-esterified fatty acids (NEFA). Therefore, the inter-organ transport of fatty acids is accomplished mostly by the circulation of NEFA, which in turn, assumes a key role as a reserve of readily available energy to peripheral tissues in the growing ruminant (Drackley, 2005). In contrast to growing animals, circulating NEFA concentrations in the plasma of mature cows can be associated with the catabolism of body fat to supply metabolic needs of the organism rather than dietary supply of lipids (Wathes et al., 2007). The concentrations of NEFA in the plasma could be of great importance as an indicator of energy delivery to peripheral tissues. Interestingly, negative associations between NEFA and RFI have been found in growing heifers (Kelly et al., 2010) and mature pregnant cows (Wood et al., 2014). These findings appear to be physiologically relevant

when taking the premise that greater concentrations of NEFA may be associated with increased energy delivery to peripheral tissues in growing animals, and are suggestive that the ability to mobilize fat, by mature pregnant cows, may play an important role in feed efficiency.

1.7.3.3. Glucose

In ruminants, during the process of pre-gastric fermentation, more readily digestible, non-structural carbohydrates (i.e., sugar and starch) are subjected to microbial fermentation in the reticulo-rumen before becoming available to the amyloytic digestion and absorption in the small intestine. This leads ruminants to depend almost exclusively on gluconeogenesis in the liver and, to a lesser extent, kidneys for their tissue glucose requirements (Weeks, 1979). Notably, the principal precursor for hepatic gluconeogenesis is propionate, one of the major volatile fatty acid byproducts of pre-gastric fermentation, which is absorbed via the ruminal epithelium into portal venous blood and almost completely removed by the liver (Elliot, 1980). Additionally, other products from pre-gastric fermentation such as acetate and 3-hydroxybutyrate (derived mostly from hydroxylation of ruminal butyrate), are major substrates for oxidation in tissues such as kidneys, heart and skeletal muscle (Weeks, 1979). Altogether, these factors contribute to the fact that most ruminant tissues, including muscle and adipose tissue, have evolved the capacity to substantially substitute VFA and their derivative ketoacids for glucose as respiratory fuel or lipogenic substrate (Bell and Bauman, 1997).

However, even though ruminants typically do not absorb great amounts of glucose from dietary intake, glucose supply is still crucial for maintenance and productive functions in ruminants, as it is an indispensable metabolic fuel for other tissues in the body, such as the brain and the liver (Weeks, 1979; Bell, 1980). Previous studies examining the relationship between RFI and blood metabolites suggested that glucose utilization and metabolism might be associated with

differences in RFI (Richardson et al., 2004; Kelly et al., 2010). However, there is still much contradiction among results. Kolath et al. (2006) reported that glucose concentration was lower in feed efficient steers, while Fitzsimons et al. (2014) did not report any differences in glucose concentrations among efficiency groups of growing heifers.

1.8. Research hypothesis and objectives

It is hypothesized that animal size, feeding behavior and blood metabolites related to protein and lipid metabolism may be associated with feed efficiency considering the energy and protein metabolism linkage between these factors. These relationships may differ according to both animal stage and to the efficiency measurement used. Thus, the evaluation of linear body measurements, feeding behavior patterns, and analyses of plasma metabolites may provide new insights and reveal basic aspects of efficiency of feed utilization that could be later used as indirect assessments of feed efficiency. Additionally, the evaluation of linear body measurements may enable improvements in prediction models of feed intake and growth.

To evaluate the hypothesis, three experiments were conducted with the objectives to:

1) Evaluate the inclusion of animal size traits in feed efficiency prediction models;
2) Investigate the relationship between linear body measurements, feeding behavior, and plasma metabolites with different measures of feed efficiency in growing heifers and steers, and mature pregnant cows;
3) Determine the differences in body measurements, feeding behavior, and plasma metabolites in animals diverging in feed efficiency measured through residual feed intake.

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2. RELATIONSHIPS BETWEEN ANIMAL SIZE, FEEDING BEHAVIOR, PLASMA METABOLITES AND FEED EFFICIENCY IN BEEF CATTLE: I. GROWING HEIFERS AND FINISHING STEERS

2.1. Introduction

The optimization of production of animal products in relation to the amount of feedstuffs fed to animals could bring significant increases in profits of production systems (Arthur and Herd, 2005) and represent positive impacts on the environment (Nkrumah et al., 2006). Thus, the improvement of feed efficiency has been a great focus of interest to the beef industry. Feed efficiency can be assessed through a variety of different measures (Swanson and Miller, 2008) that have been utilized extensively in growing beef cattle including: gain to feed (G:F; Swanson et al., 2014), residual gain (RG; Koch et al., 1963); and residual feed intake (RFI; Koch et al., 1963; Montanholi et al., 2009). Regardless of efficiency measure, the biological basis associated with the variation in efficiency of feed utilization has not been completely elucidated in livestock species. A better understanding of the biological basis associated with feed efficiency might result in the improvement of prediction models of gain and intake (Wood et al., 2014), in the evaluation of correlated response to selection (Fontoura et al., 2016), and with the identification of traits that are less expensive to measure than feed intake and efficiency (Wheadon et al., 2014).

Body size has both biological and economic effects on the efficiency of animal production (Dickerson, 1978). Furthermore, the measurement of linear body dimensions may also provide a non-invasive estimate and insights into changes in maintenance energy requirements and surface area and gut capacity (Kleiber, 1961) due to its strong associations with BW fluctuations (Heinrichs et al., 1992). Measurements of girth have been suggested to be associated with feed efficiency (Wood et al., 2014), and may represent an important inclusion in prediction models of

RFI and RG. Feeding patterns and activity could influence feed efficiency (Richardson and Herd, 2004), as animal behavioral responses can alter physical activity and thus influence total energy expenditure and impact digestive efficiency (Susenbeth et al., 1998). It is suggested that more feed efficient cattle typically engage in less daily feeding activity (Golden et al., 2008), eat smaller meals (Montanholi et al., 2010), and visit the feeder less often (Kelly et al., 2010; Montanholi et al., 2010). Blood analytes have been extensively examined to improve the understanding of the metabolic basis of efficiency of feed utilization in cattle (Basarab et al., 2003; Nkrumah et al., 2007; Gonano et al., 2014). Metabolites such as urea, non-esterified fatty acids and glucose are involved in carbohydrate, protein and lipid metabolism and might reveal basic aspects of the biological differences in feed efficiency. The concentration of these metabolites is highly dependent on level of DM intake, diet composition and productive priorities of the animal (Huntington, 1986; NRC, 2016), which are important players when considering the energetic basis of efficiency of feed utilization.

We hypothesized that feeding behavior, animal size and plasma metabolic markers are associated with different measures of feed efficiency and may display differences in relation to efficiency phenotypes, measured through RFI. Additionally, the inclusion of animal size measurements into prediction models of gain and intake may enable improvements in the accuracy of prediction models of feed intake and efficiency. The objectives of this study were to 1) evaluate the inclusion of animal size traits in feed efficiency prediction models of growing animals; 2) evaluate the association between feeding behavior, animal size and plasma metabolites with different measures of feed efficiency in growing heifers and finishing steers; and 3) determine the differences in feeding behavior, animal size and plasma metabolites in animals diverging in feed efficiency measured through three different models of RFI.

2.2. Materials and methods

2.2.1. Animals, experimental conditions and dietary treatments

During the summer of 2015 and 2016, 162 crossbred heifers were part of a 2-year experiment and were tested over a 106-day experiment (year 1 = 89; year 2 = 73). Similarly, during the spring of 2016, 62 steers were tested over a 112-day experiment. All procedures were approved by the North Dakota State University Animal Care and Use Committee. Animals were housed at the Beef Cattle Research Complex (North Dakota State University, Fargo, United States). Heifers were placed into pens of 20 to 22 animals per pen, while steers were equally divided into two pens of 31 animals. The pens had dimensions of 15.24 m x 56.39 m and gave access to an outdoor yard, as well as an indoor feeding area equipped with 8 Insentec electronic feeding stations (Hokofarm Group B. V., Marknesse, The Netherlands). Prior to all the experiments, a radio frequency ID tag was placed in the right ear allowing the recording of feed intake and behavioral measurements. A 14-day adaptation period occurred to provide animal acclimation to the research facility and the automated feeding system. Heifers were fed a forage-based diet (Table 2.1) twice a day that allowed for *ad libitum* consumption, first between 0830 h and 0930 h followed by a second feeding between 1430 h and 1530 h. In year 1 of the heifer experiment, the diet had to be reformulated because of a lack of silage supply. Steers were fed a corn-based diet (Table 2.2), with two levels of vitamin A supplementation, once a day, between 0830 h and 0930 h, that allowed for *ad libitum* consumption. The steers' dietary treatments are explained in detail by Knuston et al. (2017). Briefly, the low vitamin A diet contained 723 IU of vitamin A/kg of DM, the control treatment was supplemented with 2,200 IU of vitamin A/kg of DM, which is the NRC (2016) recommendations of vitamin A for finishing cattle.

At the beginning and end of each feeding experiment, a 2-day BW and measurements of animal size were collected. For the heifer experiment, BW and blood samples were collected every 14 days and for the steer experiment every 28 days prior to feed delivery.

Table 2.1. Ingredient and nutrient composition of TMR in growing heifers.

Item (% DM)	Year 1		Year 2
	Diet 1	Diet 2	Diet
Ingredient			
Hay	78.50	88.40	78.50
Corn silage	16.50	0.00	16.50
Corn, dry rolled	0.00	6.60	0.00
Corn, fine ground	1.92	1.92	1.92
DDGS[1]	1.93	1.93	1.93
Supplement[2]	2.00	2.00	2.00
Chemical composition			
DM	73.70	77.70	73.30
CP	10.53	11.02	12.27
NDF	59.82	63.61	62.01
ADF	35.15	34.70	35.41
Ca	0.46	0.35	0.41
P	0.33	0.29	0.27

[1]Dried distiller's grains with solubles.
[2]Supplement contained urea, salt, monensin (176.4 g/kg premix, Elanco, Greenfield, IN), vitamin premix, and a trace mineral premix.

Table 2.2. Ingredient and nutrient composition of TMR in finishing steers.

Item (% DM)	Control	Low Vitamin A
Ingredient		
Wheat straw	10.00	10.00
Corn	60.00	60.00
CSB[1]	5.00	5.00
DDGS[2]	20.00	20.00
Supplement[3]	5.00	5.00
Trace mineral premix	0.05	0.05
Vitamin A	0.007	0.00
Vitamin D	0.0007	0.00
Chemical composition		
DM	86.43	86.43
CP	14.70	14.70
NDF	25.50	25.50
ADF	10.30	10.30
Ca	1.01	1.01
P	0.53	0.53

[1]Concentrated separator by-product (partially de-sugared beet molasses).
[2]Dried distiller's grains with solubles.
[3]Supplement contained ground corn, limestone, urea, salt, monensin (176.4 g/kg premix, Elanco, Greenfield, IN), tylosin (88.2g/kg premix, Elanco, Greefield, IN).

2.2.2. Feed analysis

Similar to Swanson et al. (2014), diet samples were collected weekly. Samples were dried in a 55°C oven and ground to pass a 1-mm screen. The samples were analyzed for DM, ash, nitrogen (N; Kjehldahl method), calcium, and phosphorus by standard procedures (AOAC, 1990) and for NDF (assayed with heat stable amylase and sodium sulfite and expressed inclusive of residual ash) and ADF (expressed inclusive of residual ash) concentration by the method of Robertson and Van Soest (1981) using a fiber analyzer (Ankom Technology Corp., Fairport, USA). Percent crude protein (CP) was calculated by multiplying N concentration × 6.25.

2.2.3. Productive performance and feed efficiency assessments

Individual feed intake was determined using the Insentec automated feeding system (Hokofarm Group B. V., Marknesse, The Netherlands). At the end of each experiment, feed intake data was downloaded and used to calculate the average daily feed intake (DMI; kg/d) over the entire period. Firstly, the feed intake data was filtered in order to exclude outlier records or days where mechanical problems potentially occurred, as previously described by Mader et al. (2009). Average daily gain (ADG; kg/d) was computed as the coefficient of linear regression of body weight on time of measurement. In addition, both daily DMI and ADG were calculated as a percentage of mid-point BW (DMIrbw, ADGrbw; %). The gain to feed ratio (G:F; ratio) was calculated as a ratio of ADG:DMI during the experiments' duration. Both residual gain (RG), and residual feed intake (RFI) were modeled three different ways. The first (RG_{Koch} and RFI_{Koch}) were based on the models described by Koch et al. (1963), the second (RG_{us} and RFI_{us}) were based on the RFI models adjusted for body composition traits as proposed by Montanholi et al. (2009) and the third (RG_{size} and RFI_{size}) were adjusted for both body composition and animal size traits. All the RG and RFI models were calculated using the ordinary least squares (GLM procedure; SAS Institute Inc., Cary, USA), using year (in the case of the heifer experiment), mid-point $BW^{0.75}$, feed intake, body and carcass composition, and animal size measurements collected over the duration of the trial. Overall, predicted gains were calculated as:

$$ADG = \beta_0 + \beta_1(\text{mmBW; kg}) + \beta_2(\text{DMI; kg}) + \beta_3 \ldots \beta_n(\text{body or carcass composition traits})$$

$$+ \beta_{n+1} \ldots \beta_z(\text{animal size traits}) + \text{RG models } (RG_{Koch}, RG_{us} \text{ or } RG_{size})$$

Where β_0 is the regression intercept, β_1 is the coefficient of regression for mid-point metabolic body weight, β_2 is the coefficient of regression for dry matter intake, $\beta_3 \ldots \beta_n$, are the models' best fit body or carcass composition traits, $\beta_{n+1} \ldots \beta_z$ are the models' best fit animal size

traits. RG_{Koch}, RG_{us} or RG_{size} were the residue of this regression, and were used accordingly to each model. The selection criteria for each model across all experiments were based on the Bayesian information criterion (BIC) and R^2.

Overall, predicted intakes were calculated as:

$$DMI = \beta_0 + \beta_1(\text{mmBW; kg}) + \beta_2(\text{ADG; kg}) + \beta_3 \ldots \beta_n(\text{body or carcass composition traits}) + \beta_{n+1} \ldots \beta_z(\text{animal size traits}) + \text{RFI models } (RFI_{Koch}, RFI_{us} \text{ or } RFI_{size})$$

Where β_0 is the regression intercept, β_1 is the coefficient of regression for mid-point metabolic body weight, β_2 is the coefficient of regression for average daily gain, $\beta_3 \ldots \beta_n$, are the models' best fit body or carcass composition traits, $\beta_{n+1} \ldots \beta_z$ are the models' best fit animal size traits. RFI_{Koch}, RFI_{us} or RFI_{size} were the residue of this regression, and were used accordingly to each model. The selection criteria for each model across all experiments were based on the BIC and R^2.

2.2.4. Body composition determinations

For the heifer experiment, carcass ultrasounds were performed using an Aloka SSD-500 ultrasound unit (model 5044; 172 mm; 3.5 MHz; Corometrics Medical Systems, Wallingford, USA) equipped with a 17-cm linear array transducer. Measurements were performed on initial and final days of the feeding trials and consisted of *longissimus* muscle area (rib eye area, cm^2), four independent images collected laterally between the 12^{th} and 13^{th} ribs to estimate the percentage of intramuscular fat within the *longissimus dorsi* muscle (intramuscular fat, %), subcutaneous fat depth over the *longissimus* muscle in the fourth quadrant distal to the spine (rib fat thickness, mm), and fatness at the termination point of the *biceps femoris* muscle (rump fat, mm).

For the steer experiment, animals were slaughtered at a commercial abattoir (Tyson Fresh Meats, Dakota City, NE) at an average of 58 ± 14 days after completion of the feeding trial. Carcass

composition traits were then collected by camera data at the plant and this data included yield grade (range 1 to 5), kidney pelvic heart fat (%); and with the assistance of computer image analysis, marbling score (range 400 to 599; 400 – 399, small; 500 – 599, modest), area of the *longissimus* muscle (ribeye area, cm^2) and subcutaneous fat (cm).

2.2.5. Feeding behavior and animal size assessments

Feeding behavior traits were calculated similar to Swanson et al. (2014) and were summarized as: events (per day; number of bunk visits and meals), eating time (minutes; per visit, per meal, and per day), and eating rate (grams of DM; per visit and per meal). A visit was defined as each time the Insentec system detect an animal at a bunk, while a meal was defined as eating periods that might include short breaks separated by intervals not longer than 7 min (Forbes, 1995; Montanholi et al., 2010). The data were summarized as the average of each individual animal from the initial day until the last day of the experiment.

Body measurements were recorded similar to as described by Wood et al. (2014). Body length was defined as the distance from the point of shoulder to end of the rump, hip height was defined as the distance from ground to base of tail head and hip width the distance between the *crista iliaca*. For the girth measurements, heart girth was measured as the circumference around the midsection caudal to shoulder, mid-girth was measured as the circumference around middle over navel, and flank girth was measured as the circumference around the middle at the flank. Additionally, in the heifer experiment, the flank girth was measured cranially to the udder. Body length, girth measures and hip width were recorded using a fabric measuring tape, and hip height measurements were recorded with a livestock height measuring stick.

2.2.6. Plasma metabolic markers

Blood samples were collected by jugular venipuncture while the animals were individually restrained in a squeeze chute. Blood was collected using 1.1 x 25 mm blood collection needles (BD Vacutainer® Precision Glide, BD Inc., Franklin Lakes, USA) and 10 mL sodium heparin blood collection tubes (BD Vacutainer®, BD Inc., Franklin Lakes, USA). Immediately after collection, samples were kept at 4°C until centrifugation. The samples were centrifuged at 4 °C at 3000×g for 20 minutes. The plasma was decanted into three 2-mL micro centrifuge tubes and stored at -20°C until analysis. Urea concentration in plasma (PUN) was measured by the QuantiChrom™ Urea Assay Kit (BioAssay Systems, Hayward, USA) and was determined using the urease/Berthelot procedure (Chaney and Marbach, 1962; Fawcett and Scott, 1960). Non-esterified fatty acid (NEFA) concentration was analyzed using the acyl-CoA synthetase-acyl-CoA oxidase method using a kit from Wako Pure Chemical Industries (Dallas, TX). Glucose concentration was measured using the Infinity Glucose Hexokinase kit (Thermo Trace, Louisville, USA) and was analyzed using the hexokinase/gluxose-6-phosphate dehydrogenase method (Farrance, 1987). All assays were performed using a 96-well microplate reader (Synergy, HI Microplate Reader, BioTek Instruments, Winooski, VT).

2.2.7. Statistical analysis

For both experiments, the individual animal (heifer or steer) was considered an independent variable and was evaluated as a random effect, RFI groups (high- and low-) in the three prediction models (RFI_{Koch}, RFI_{us} and RFI_{size}) and day were treated as fixed effects, and the interaction between day and RFI group was treated as a random effect. Productive performance, body and carcass composition, feeding behavior, animal size and plasma metabolic markers were the response variables evaluated. Statistical analysis was performed using the SAS® software (version

9.4; SAS Institute Inc., Cary, USA). Prior to statistical analysis, normality was tested and ensured through residuals' diagnostic plots using the ordinary least squares. If needed, transformations were performed and values were back-transformed to be reported. A categorical analysis was carried out in order to compare the animals according to RFI values within each determination model (RFI_{Koch}, RFI_{us} and RFI_{size}). Means of the two RFI groups (high- and low-) in each of the models (RFI_{Koch}, RFI_{us} and RFI_{size}) for body and carcass composition, feeding behavior and animal size traits were tested using the general linear model of SAS, while the means for plasma metabolic markers were tested using the mixed procedure of SAS. The covariance structures used to test fit statistics of the mixed model included variance components, compound symmetry, autoregressive one, unstructured, and ante-dependence one. Smaller fit values (BIC) were always selected. The least square means comparisons for analysis conducted using both the general linear model and mixed model were performed using the Scheffé's test. The associations between body and carcass composition, feeding behavior, animal size and blood metabolites with productive performance traits were measured through partial correlations, adjusted for year (heifer experiment) and dietary treatment (steer experiment), using the MANOVA/PRINTE statement of the general linear model. For all analyses, data were considered statistically significant when $P \leq 0.05$ and were considered a trend towards significance when $0.10 \geq P > 0.05$.

2.3. Results

2.3.1. Prediction models

The goodness of fit (R^2, CV, R MSE) for regression models of intake (RFI_{Koch}, RFI_{us} and RFI_{size}) and gain (RG_{Koch}, RG_{us} and RG_{size}) can be found in Table 2.3. The addition of size traits in the intake prediction model (RFI_{size}) increased the accuracy of prediction from 3 to 4% in the models accounting for BW and BW gain (RFI_{Koch}), and approximately 0 to 3% in the models that

were adjusted to body or carcass composition (RFI_{us}). Similarly and more drastically, the addition of size traits in the gain prediction model (RG_{size}) increased the accuracy of prediction from 1 to 12 % and 1 to 11% in comparison to RG_{Koch} and RG_{us} models, respectively.

Table 2.3. Model fit statistics for the selected residual feed intake (DMI models) and residual gain (ADG models) with differing covariates over the different experiments.

Experiment	Model covariates[†]	N	R^2	CV	R MSE
Heifers	Residual feed intake				
	RFI_{Koch}: yr mmBW ADG	162	0.66	8.28	0.75
	RFI_{us}: yr mmBW ADG mIMFT mRBEA mRBFT mRUMP	162	0.67	8.23	0.75
	RFI_{size}: yr mmBW ADG mIMFT mRBEA iHG iMG	162	0.66	8.35	0.76
	Residual gain				
	RG_{Koch}: yr mmBW DMI	162	0.55	18.52	0.12
	RG_{us}: yr mmBW DMI mRBFT	162	0.55	18.57	0.13
	RG_{size}: yr mmBW DMI mRBFT iMG	162	0.55	18.61	0.13
Steers	Residual feed intake				
	RFI_{Koch}: mmBW ADG	61	0.72	6.80	0.74
	RFI_{us}: mmBW ADG BKFT	58	0.72	6.75	0.74
	RFI_{size}: mmBW ADG RBEA KPH iHW iMG	57	0.75	6.62	0.73
	Residual gain				
	RG_{Koch}: mmBW DMI	61	0.44	7.53	0.11
	RG_{us}: mmBW DMI BKFT	58	0.46	7.31	0.11
	RG_{size}: mmBW DMI BKFT iHG iMG	57	0.54	6.84	0.10

[†]mmBW, mid-point $BW^{0.75}$; mIMFT, mid-point intramuscular fat; mRBEA, mid-point rib eye area; mRBFT, mid-point rib fat; mRUMP, mid-point rump fat; iHG, initial heart girth; iMG, initial mid girth; iHW, initial hip width; BKFT, back fat thickness; RBEA, rib eye area; KPH, kidney pelvic heart fat.

Table 2.4. Least square means of productive performance traits, measured in growing heifers, by high- and low-RFI groups according to the three RFI determination models (RFI_{Koch}, RFI_{us} and RFI_{size}).

Traits (unit)	RFI_{Koch}			RFI_{us}			RFI_{size}		
	high-RFI†	low-RFI†	*P*	high-RFI†	low-RFI†	*P*	high-RFI†	low-RFI†	*P*
Initial BW (kg)	341 ± 5.30	343 ± 4.74	0.69	340 ± 5.23	344 ± 4.79	0.59	342 ± 5.20	342 ± 4.82	0.93
Final BW (kg)	410 ± 6.60	413 ± 5.91	0.79	410 ± 6.51	413 ± 5.97	0.70	413 ± 6.47	410 ± 6.01	0.75
Average daily gain (kg/d)	0.67 ± 0.02	0.67 ± 0.02	0.94	0.67 ± 0.02	0.67 ± 0.02	1.00	0.69 ± 0.02	0.66 ± 0.02	0.36
Average daily gain relative to BW (%)	0.18 ± 0.01	0.18 ± 0.01	0.90	0.18 ± 0.01	0.18 ± 0.01	0.97	0.18 ± 0.01	0.17 ± 0.01	0.87
Dry matter intake (kg)	9.66 ± 0.14	8.60 ± 0.12	0.01	9.61 ± 0.14	8.62 ± 0.13	0.01	9.64 ± 0.14	8.58 ± 0.13	0.01
Dry matter intake relative to BW (%)	2.58 ± 0.05	2.28 ± 0.07	0.01	2.57 ± 0.05	2.28 ± 0.08	0.01	2.56 ± 0.03	2.29 ± 0.05	0.01
Gain to feed (ratio)	0.07 ± 0.002	0.08 ± 0.002	0.01	0.07 ± 0.002	0.08 ± 0.002	0.01	0.07 ± 0.002	0.08 ± 0.002	0.06
RG (Koch et al., 1963) (RG_{Koch}, kg/d)	-0.02 ± 0.01	0.02 ± 0.01	0.04	-0.02 ± 0.01	0.02 ± 0.01	0.04	-0.01 ± 0.01	0.01 ± 0.01	0.15
RG (ultrasound traits) (RG_{us}, kg/d)	-0.02 ± 0.01	0.02 ± 0.01	0.03	-0.02 ± 0.01	0.02 ± 0.01	0.03	-0.01 ± 0.01	0.01 ± 0.01	0.16
RG (size adjusted) (RG_{size}, kg/d)	-0.02 ± 0.01	0.01 ± 0.01	0.08	-0.02 ± 0.01	0.01 ± 0.01	0.09	-0.01 ± 0.01	0.01 ± 0.01	0.15
RFI (Koch et al., 1963) (RFI_{Koch}, kg/d)	0.61 ± 0.06	-0.49 ± 0.05	0.01	0.58 ± 0.06	-0.48 ± 0.06	0.01	0.55 ± 0.06	-0.47 ± 0.06	0.01
RFI (ultrasound traits) (RFI_{us}, kg/d)	0.58 ± 0.06	-0.48 ± 0.05	0.01	0.58 ± 0.06	-0.50 ± 0.05	0.01	0.55 ± 0.06	-0.49 ± 0.06	0.01

Table 2.4. Least square means of productive performance traits, measured in growing heifers, by high- and low-RFI groups according to the three RFI determination models (RFI_{Koch}, RFI_{us} and RFI_{size}) (continued).

Traits (unit)	RFI_{Koch}			RFI_{us}			RFI_{size}		
	high-RFI[†]	low-RFI[†]	*P*	high-RFI[†]	low-RFI[†]	*P*	high-RFI[†]	low-RFI[†]	*P*
RFI (size adjusted) (RFI_{size}, kg/d)	0.54 ± 0.06	-0.43 ± 0.05	0.01	0.54 ± 0.06	-0.45 ± 0.05	0.01	0.55 ± 0.06	-0.48 ± 0.05	0.01

[†]Mean ± SEM.

RG = residual gain; RFI = residual feed intake.

Table 2.5. Least square means of productive performance, measured in finishing steers, by high- and low-RFI groups according to the three RFI determination models (RFI_{Koch}, RFI_{us} and RFI_{size}).

Traits (unit)	RFI_{Koch}			RFI_{us}			RFI_{size}		
	high-RFI†	low-RFI†	*P*	high-RFI†	low-RFI†	*P*	high-RFI†	low-RFI†	*P*
Initial BW (kg)	397 ± 9.82	406 ± 10.35	0.52	398 ± 10.22	404 ± 10.09	0.66	394 ± 10.15	408 ± 10.18	0.32
Final BW (kg)	596 ± 11.98	609 ± 12.39	0.48	599 ± 12.25	607 ± 12.25	0.63	594 ± 12.39	610 ± 12.21	0.36
Average daily gain (kg/d)	1.48 ± 0.03	1.50 ± 0.03	0.73	1.47 ± 0.03	1.50 ± 0.03	0.44	1.49 ± 0.03	1.49 ± 0.03	0.93
Average daily gain relative to BW (%)	0.30 ± 0.12	0.30 ± 0.15	0.90	0.30 ± 0.10	0.30 ± 0.10	0.97	0.30 ± 0.15	0.30 ± 0.17	0.95
Dry matter intake (kg)	11.38 ± 0.23	10.39 ± 0.24	0.01	11.38 ± 0.24	10.46 ± 0.23	0.01	11.35 ± 0.24	10.45 ± 0.24	0.01
Dry matter intake relative to BW (%)	2.30 ± 0.07	2.08 ± 0.09	0.17	2.31 ± 0.10	2.09 ± 0.11	0.20	2.31 ± 0.05	2.08 ± 0.07	0.22
Gain to feed (ratio)	0.13 ± 0.002	0.14 ± 0.002	0.01	0.13 ± 0.002	0.14 ± 0.002	0.01	0.13 ± 0.002	0.14 ± 0.002	0.01
RG (Koch et al., 1963) (RG_{Koch}, kg/d)	-0.04 ± 0.02	0.05 ± 0.02	0.01	-0.05 ± 0.02	0.05 ± 0.02	0.01	-0.04 ± 0.02	0.04 ± 0.02	0.01
RG (ultrasound traits) (RG_{us}, kg/d)	-0.05 ± 0.02	0.04 ± 0.02	0.01	-0.06 ± 0.02	0.05 ± 0.02	0.01	-0.04 ± 0.02	0.03 ± 0.02	0.01
RG (size adjusted) (RG_{size}, kg/d)	-0.04 ± 0.02	0.04 ± 0.02	0.01	-0.05 ± 0.02	0.04 ± 0.02	0.01	-0.04 ± 0.02	0.03 ± 0.02	0.01
RFI (Koch et al., 1963) (RFI_{Koch}, kg/d)	0.53 ± 0.08	-0.59 ± 0.09	0.01	0.57 ± 0.09	-0.55 ± 0.09	0.01	0.54 ± 0.09	-0.54 ± 0.09	0.01
RFI (ultrasound traits) (RFI_{us}, kg/d)	0.52 ± 0.09	-0.55 ± 0.09	0.01	0.59 ± 0.08	-0.55 ± 0.08	0.01	0.54 ± 0.09	-0.52 ± 0.09	0.01
RFI (size adjusted) (RFI_{size}, kg/d)	0.48 ± 0.09	-0.53 ± 0.09	0.01	0.54 ± 0.09	-0.51 ± 0.08	0.01	0.53 ± 0.08	-0.54 ± 0.08	0.01

†Mean ± SEM.

RG = residual gain; RFI = residual feed intake.

Table 2.6. Least square means of body composition traits, measured in growing heifers, by high- and low-RFI groups according to the three RFI determination models (RFI_{Koch}, RFI_{us} and RFI_{size}).

Traits (unit)	RFI_{Koch}			RFI_{us}			RFI_{size}		
	high-RFI†	low-RFI†	*P*	high-RFI†	low-RFI†	*P*	high-RFI†	low-RFI†	*P*
Initial intramuscular fat (%)	3.56 ± 0.09	3.49 ± 0.08	0.56	3.54 ± 0.08	3.51 ± 0.08	0.77	3.49 ± 0.08	3.55 ± 0.08	0.57
Initial rib eye area (cm^2)	49.37 ± 0.86	50.73 ± 0.77	0.24	49.79 ± 0.85	50.41 ± 0.78	0.59	49.86 ± 0.85	50.36 ± 0.79	0.66
Initial backfat thickness (mm)	6.68 ± 0.17	6.78 ± 0.15	0.67	6.69 ± 0.17	6.77 ± 0.15	0.73	6.68 ± 0.17	6.78 ± 0.16	0.66
Initial rump fat (mm)	4.06 ± 0.16	4.24 ± 4.24	0.41	4.14 ± 0.16	4.17 ± 0.14	0.88	4.00 ± 0.15	4.30 ± 0.14	0.15
Final intramuscular fat (%)	3.59 ± 0.09	3.52 ± 0.08	0.51	3.60 ± 0.09	3.51 ± 0.08	0.45	3.57 ± 0.09	3.54 ± 0.08	0.79
Final rib eye area (cm^2)	56.73 ± 0.93	58.32 ± 0.84	0.21	57.69 ± 0.93	57.55 ± 0.85	0.91	57.65 ± 0.92	57.58 ± 0.85	0.96
Final backfat thickness (mm)	7.61 ± 0.19	7.66 ± 0.17	0.85	7.65 ± 0.18	7.63 ± 0.17	0.93	7.60 ± 0.18	7.67 ± 0.17	0.79
Final rump fat (mm)	5.22 ± 0.20	5.02 ± 0.18	0.44	5.30 ± 0.20	4.95 ± 0.18	0.20	5.15 ± 0.20	5.07 ± 0.18	0.77

†Mean ± SEM.

Table 2.7. Least square means of carcass quality traits, measured in finishing steers, by high- and low-RFI groups according to the three RFI determination models (RFI_{Koch}, RFI_{us} and RFI_{size}).

Traits (unit)	RFI_{Koch}			RFI_{us}			RFI_{size}		
	high-RFI†	low-RFI†	*P*	high-RFI†	low-RFI†	*P*	high-RFI†	low-RFI†	*P*
Calculated yield grade (1 to 5)	2.92 ± 0.13	2.81 ± 0.13	0.54	2.80 ± 0.13	2.94 ± 0.13	0.44	2.87 ± 0.13	2.91 ± 0.13	0.83
Marbling (score, 400 to 599)	521 ± 19.64	496 ± 21.06	0.41	517 ± 20.55	502 ± 20.55	0.63	516 ± 19.98	510 ± 20.38	0.84
Rib eye area (cm^2)	34.85 ± 0.76	36.47 ± 0.82	0.16	35.39 ± 0.81	35.81 ± 0.81	0.72	34.96 ± 0.79	36.06 ± 0.80	0.34
Backfat thickness (cm)	1.14 ± 0.07	1.03 ± 0.07	0.24	1.06 ± 0.07	1.12 ± 0.07	0.58	1.10 ± 0.07	1.10 ± 0.07	1.00
Kidney pelvic heart fat (cm)	1.86 ± 0.04	1.78 ± 0.04	0.18	1.83 ± 0.04	1.81 ± 0.04	0.65	1.84 ± 0.04	1.81 ± 0.04	0.61

†Mean ± SEM.

2.3.2. Productive performance and body composition

By design, the RFI_{Koch}, RFI_{us} and RFI_{size} were different between the high- and low-RFI groups in both experiments (Table 2.4, Table 2.5). This represented a difference in daily DMI of up to 1.06 kg between less efficient (high-RFI) and more efficient (low-RFI) heifers (Table 2.4), and up to 0.90 kg between high-RFI and low-RFI steers (Table 2.5), as reported for the RFI_{size} model. Additionally, all RFI models across experiments suggested that low-RFI animals possessed a better G:F ratio (Table 2.4, Table 2.5). Body composition traits of heifers (Table 2.6) and carcass composition traits of steers (Table 2.7) did not differ between the high- and low-RFI groups across the three RFI models.

The evaluation of the associations among productive performance, efficiency and body composition traits, in heifers, indicated similar correlations between ADG and DMI with initial and final intramuscular fat (ADG: r = -0.16 and r = -0.14, respectively; DMI: r = -0.23 and r = -0.19, respectively), and initial and final ribeye area (ADG: r = 0.36 and r = 0.27, respectively; DMI: r = 0.43 and r = 0.26, respectively). Low to moderate positive correlations ($P \leq 0.05$) were observed between G:F with initial (r = 0.22) and final (r = 0.17) ribeye area, while negative correlations were observed between RG_{Koch} and initial rib fat (r = -0.15). In steers, greater DMI tended to be correlated ($P \leq 0.10$) with increased carcass ribeye area (r = 0.25) and greater marbling score (r = 0.25). The RFI_{Koch} model showed a tendency ($P \leq 0.10$) for a correlation of higher RFI with increased kidney pelvic heart fat (r = 0.23).

Table 2.8. Least square means of feeding behavior traits, measured in growing heifers, by high- and low-RFI groups according to the three RFI determination models (RFI_{Koch}, RFI_{us} and RFI_{size}).

Traits (unit)	RFI_{Koch}			RFI_{us}			RFI_{size}		
	high-RFI†	low-RFI†	*P*	high-RFI†	low-RFI†	*P*	high-RFI†	low-RFI†	*P*
Meals (events/d)	25 ± 1.75	22 ± 1.56	0.14	24 ± 1.73	22 ± 1.59	0.31	23 ± 1.73	23 ± 1.60	0.96
Visits (events/d)	112 ± 3.54	85 ± 3.16	0.01	109 ± 3.59	86 ± 3.30	0.01	106 ± 3.66	88 ± 3.40	0.01
Daily time (min)	149.97 ± 4.44	159.86 ± 3.97	0.10	151.92 ± 4.40	158.45 ± 4.03	0.28	154.66 ± 4.38	156.17 ± 4.07	0.80
Time per meal (min/event)	11.84 ± 0.31	13.97 ± 0.28	0.40	11.18 ± 0.31	14.58 ± 0.28	0.18	11.40 ± 0.31	14.42 ± 0.28	0.23
Time per visit (min/event)	4.44 ± 0.13	5.3 ± 0.11	0.40	4.18 ± 0.12	5.54 ± 0.11	0.18	4.25 ± 0.12	5.49 ± 0.11	0.22
Eating rate per meal (g of DM/event)	585 ± 38.41	550 ± 34.35	0.51	600 ± 37.76	537 ± 34.63	0.22	618 ± 37.26	520 ± 34.59	0.06
Eating rate per visit (g of DM/event)	93 ± 5.19	118 ± 4.65	0.01	96 ± 5.20	116 ± 4.77	0.01	100 ± 5.24	112 ± 4.86	0.08

†Mean ± SEM.

Table 2.9. Least square means of feeding behavior traits, measured in finishing steers, by high- and low-RFI groups according to the three RFI determination models (RFI_{Koch}, RFI_{us} and RFI_{size}).

Traits (unit)	RFI_{Koch}			RFI_{us}			RFI_{size}		
	high-RFI[†]	low-RFI[†]	*P*	high-RFI[†]	low-RFI[†]	*P*	high-RFI[†]	low-RFI[†]	*P*
Meals (events/d)	10 ± 0.34	9 ± 0.36	0.09	10 ± 0.34	9 ± 0.33	0.01	11 ± 0.34	9 ± 0.35	0.02
Visits (events/d)	25 ± 0.92	22 ± 0.97	0.09	25 ± 0.91	21 ± 0.90	0.01	25 ± 0.93	22 ± 0.93	0.02
Daily time (min)	96.10 ± 2.50	90.45 ± 2.64	0.13	94.04 ± 2.65	92.82 ± 2.62	0.75	95.41 ± 2.62	91.73 ± 2.63	0.33
Time per meal (min/event)	9.54 ± 0.40	10.00 ± 0.43	0.44	9.21 ± 0.41	10.29 ± 0.40	0.07	9.40 ± 0.41	10.19 ± 0.41	0.18
Time per visit (min/event)	4.03 ± 0.19	4.31 ± 0.20	0.32	3.89 ± 0.19	4.43 ± 0.19	0.05	3.97 ± 0.19	4.40 ± 0.19	0.12
Eating rate per meal (g of DM/event)	3014 ± 125.39	2705 ± 160.55	0.17	3239 ± 145.95	2505 ± 144.04	0.01	3128 ± 151.38	2579 ± 151.38	0.01
Eating rate per visit (g of DM/event)	1128 ± 44.26	1142 ± 46.64	0.83	1107 ± 45.74	1161 ± 45.14	0.41	1110 ± 45.72	1160 ± 45.88	0.44

[†]Mean ± SEM.

2.3.3. Feeding behavior

Decreased daily visits to the bunk and faster eating rate per visit ($P \leq 0.05$) were observed in low-RFI heifers (Table 2.8). For efficient steers, daily meals ($P \leq 0.10$), visits and eating rate per meal were decreased ($P \leq 0.05$), while the amount of time spent at the bunk during a visit was increased ($P \leq 0.05$; Table 2.9).

In steers, all RFI models ($P \leq 0.05$) suggested that higher RFI was correlated with increased number of meals (range of r = 0.29 to 0.34) and visits (range of r = 0.30 to 0.33). In heifers, RFI_{Koch} and RFI_{us} were positively correlated ($P \leq 0.05$) with meals per day (r = 0.17 and r = 0.18, respectively) and visits per day (r = 0.41 and r = 0.40, respectively), while longer time spent at the bunk per day was correlated ($P \leq 0.05$) with improved BW gain (G:F: r = 0.34; RG_{Koch}: r = 0.20). Furthermore, interesting and opposite results were found in relation to the eating rate per visit and RFI_{us} ($P \leq 0.05$); in heifers, a negative correlation was found (r = -0.24), while a positive correlation was found in steers (r = 0.33).

Table 2.10. Least square means of animal size traits, measured in growing heifers, by high- and low-RFI groups according to the three RFI determination models (RFI_{Koch}, RFI_{us} and RFI_{size}).

Traits (unit)	RFI_{Koch}			RFI_{us}			RFI_{size}		
	high-RFI†	low-RFI†	*P*	high-RFI†	low-RFI†	*P*	high-RFI†	low-RFI†	*P*
Initial body length (cm)	100.46 ± 0.95	99.25 ± 0.85	0.26	100.54 ± 0.93	99.17 ± 0.85	0.12	101.28 ± 0.92	99.38 ± 0.86	0.06
Initial hip height (cm)	110.99 ± 1.11	110.57 ± 0.99	0.51	110.84 ± 1.10	110.69 ± 1.00	0.42	110.97 ± 1.09	110.58 ± 1.01	0.37
Initial hip width (cm)	41.96 ± 0.36	41.38 ± 0.32	0.22	41.86 ± 0.35	41.46 ± 0.32	0.4	42.00 ± 0.35	41.33 ± 0.32	0.16
Initial heart girth (cm)	163.98 ± 0.95	163.03 ± 0.85	0.45	163.51 ± 0.93	163.4 ± 0.86	0.93	163.75 ± 0.93	163.2 ± 0.86	0.66
Initial mid girth (cm)	195.39 ± 1.33	192.5 ± 1.19	0.11	194.59 ± 1.32	193.1 ± 1.21	0.41	194.45 ± 1.31	193.21 ± 1.22	0.49
Initial flank girth (cm)	172.76 ± 5.29	170.94 ± 4.73	0.27	172.32 ± 5.23	171.28 ± 4.79	0.53	172.05 ± 5.19	171.49 ± 4.82	0.74
Final body length (cm)	103.58 ± 1.09	102.15 ± 0.97	0.41	103.87 ± 1.08	101.87 ± 0.98	0.35	104.06 ± 1.07	101.69 ± 0.99	0.54
Final hip height (cm)	116.12 ± 0.87	115.14 ± 0.78	0.72	116.23 ± 0.86	115.02 ± 0.79	0.9	116.29 ± 0.85	114.96 ± 0.79	0.73
Final hip width (cm)	43.06 ± 0.57	42.67 ± 0.51	0.61	42.80 ± 0.56	42.88 ± 0.51	0.92	43.1 ± 0.55	42.62 ± 0.52	0.52
Final heart girth (cm)	177.98 ± 1.05	177.1 ± 0.94	0.54	177.35 ± 1.04	177.61 ± 0.95	0.86	177.58 ± 1.03	177.41 ± 0.96	0.91
Final mid girth (cm)	215.23 ± 1.59	214.57 ± 1.43	0.76	214.29 ± 1.56	215.36 ± 1.44	0.61	215.26 ± 1.55	214.53 ± 1.45	0.73
Final flank girth (cm)	225.89 ± 1.23	221.36 ± 1.10	0.52	223.94 ± 1.22	222.88 ± 1.12	0.88	222.75 ± 1.21	223.90 ± 1.12	0.87

†Mean ± SEM.

Table 2.11. Least square means of animal size traits, measured in finishing steers, by high- and low-RFI groups according to the three RFI determination models (RFI_{Koch}, RFI_{us} and RFI_{size}).

Traits (unit)	RFI_{Koch}			RFI_{us}			RFI_{size}		
	high-RFI†	low-RFI†	*P*	high-RFI†	low-RFI†	*P*	high-RFI†	low-RFI†	*P*
Initial body length (cm)	87.31 ± 0.97	86.01 ± 1.01	0.36	88.21 ± 0.98	85.24 ± 0.95	0.06	87.72 ± 0.97	85.64 ± 0.98	0.14
Initial hip height (cm)	112.2 ± 0.08	114.88 ± 1.09	0.11	112.33 ± 1.10	114.58 ± 1.07	0.15	112.24 ± 1.07	114.74 ± 1.08	0.11
Initial hip width (cm)	41.04 ± 0.68	41.92 ± 0.70	0.37	40.91 ± 0.70	41.98 ± 0.68	0.29	41.31 ± 0.69	41.61 ± 0.69	0.76
Initial heart girth (cm)	172.38 ± 1.81	172.55 ± 1.88	0.95	172.22 ± 1.88	172.69 ± 1.83	0.86	171.82 ± 1.83	173.11 ± 1.84	0.62
Initial mid girth (cm)	208.01 ± 1.95	208.5 ± 2.02	0.86	207.68 ± 2.02	208.78 ± 1.97	0.7	208.21 ± 1.98	208.28 ± 1.98	0.98
Initial flank girth (cm)	179.68 ± 2.10	181.34 ± 2.19	0.59	181.4 ± 2.19	179.60 ± 2.13	0.56	180.34 ± 2.14	180.62 ± 2.15	0.93
Final body length (cm)	116.66 ± 1.28	118.18 ± 1.32	0.41	116.76 ± 1.30	118.02 ± 1.30	0.5	116.09 ± 1.31	118.77 ± 1.29	0.15
Final hip height (cm)	120.37 ± 1.21	122.55 ± 1.26	0.22	120.78 ± 1.25	122.07 ± 1.25	0.47	120.5 ± 1.25	122.04 ± 1.23	0.39
Final hip width (cm)	47.68 ± 0.56	48.31 ± 0.58	0.44	47.75 ± 0.57	48.22 ± 0.57	0.56	47.59 ± 0.58	48.31 ± 0.57	0.39
Final heart girth (cm)	201.08 ± 1.70	200.57 ± 1.75	0.84	201.30 ± 1.73	200.36 ± 1.73	0.7	200.89 ± 1.76	200.73 ± 1.74	0.95
Final mid girth (cm)	232.33 ± 2.32	231.03 ± 2.39	0.7	232.32 ± 2.36	231.08 ± 2.36	0.72	231.9 ± 2.40	231.80 ± 2.36	0.98
Final flank girth (cm)	198.47 ± 1.62	199.06 ± 1.68	0.8	198.62 ± 1.66	198.89 ± 1.66	0.91	198.09 ± 1.68	199.41 ± 1.66	0.58

†Mean ± SEM

2.3.4. Animal size

Despite a few tendencies towards significance in relation to decreased body length in efficient heifers (Table 2.10) and steers (Table 2.11), animal size traits did not differ between efficiency groups across all RFI models. All animal size traits were positively correlated ($P \leq 0.05$) with ADG (heifer experiment, range: r = 0.17 to r = 0.44; steer experiment, range: r = 0.22 to r = 0.54) and DMI (heifer experiment, range: r = 0.27 to r = 0.47; steer experiment, range: r = 0.25 to r = 0.88). The RFI_{Koch}, RFI_{us} and RFI_{size} models did not display any correlation with animal size traits ($P > 0.10$). However, G:F was correlated ($P \leq 0.05$) with initial and final heart girth (heifer experiment, r = 0.16 and r = 0.28, respectively; steer experiment, r = -0.56 and r = -0.53, respectively); and in heifers, final mid-girth was positively associated ($P \leq 0.05$) with G:F (r = 0.35), RG_{Koch} (r = 0.20) and RG_{us} (r = 0.20).

2.3.5. Plasma metabolic markers

The results for plasma metabolic markers followed the same pattern across all RFI models. Therefore, the pattern of plasma metabolic markers across the entire testing period for heifers and steers is being shown within the RFI_{size} model (Figure 2.1). Plasma urea-N (Figure 2.1A and Figure 2.1D) and glucose (Figure 2.1C and Figure 2.1F) concentrations did not differ between efficiency groups in both heifer and steer experiments. Although NEFA concentrations did not differ between efficiency groups in the steer experiment (Figure 2.1E), feed efficient heifers had greater NEFA levels ($P \leq 0.05$) when compared to inefficient heifers (Figure 2.1B).

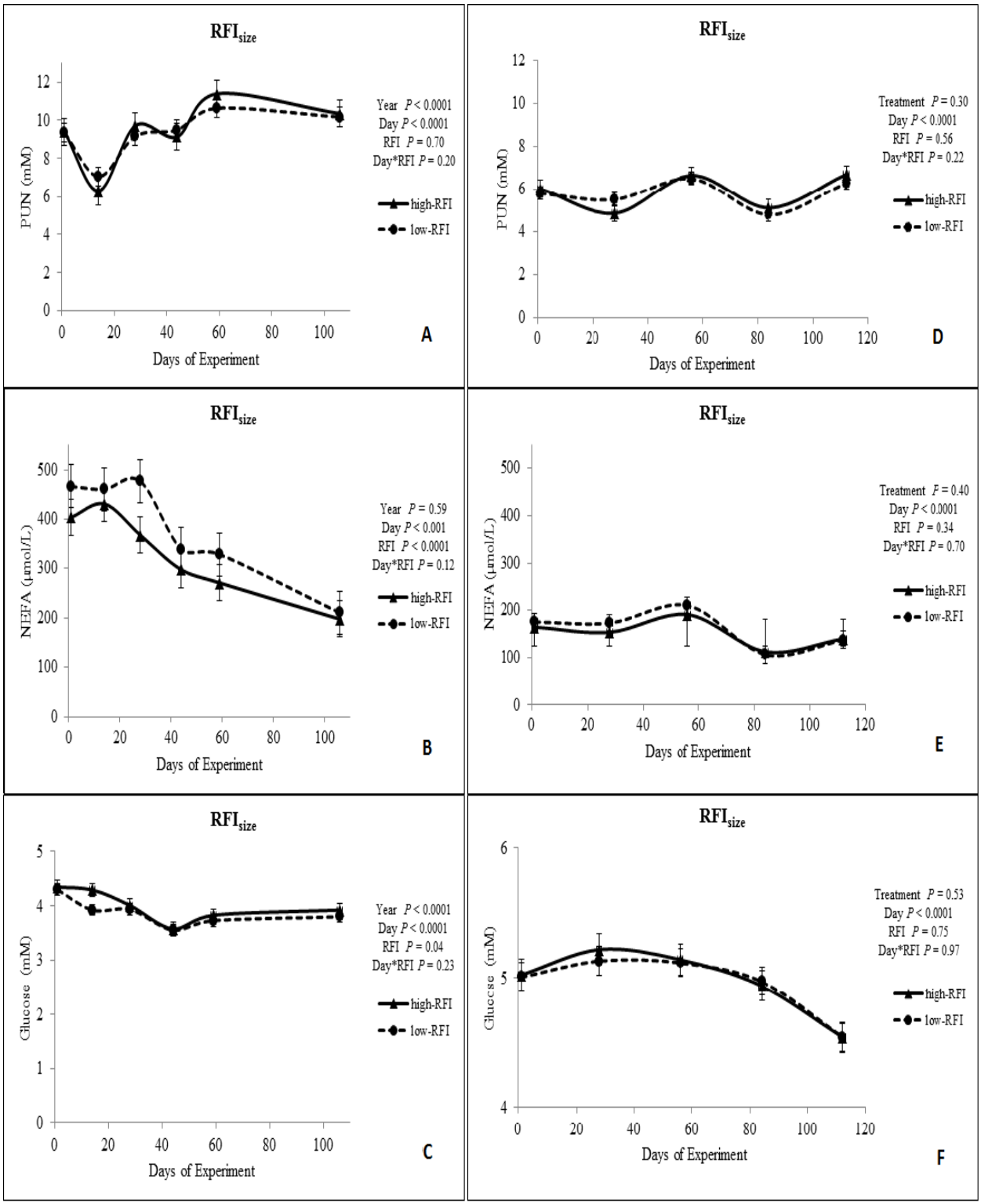

Figure 2.1. Plasma metabolites in heifers (A, B, C) and steers (D, E, F) over the performance evaluation (106 d) by feed efficiency group (RFI_{size} model, adjusted for size traits). (A, D) Plasma urea-N, (B, E) Non-esterified fatty acids and (C, F) glucose.

The averaged value over the entire experimental period for PUN was positively associated ($P \leq 0.05$) with DMI (heifer experiment, r = 0.18) and negatively associated with RFI (heifer experiment, RFI_{Koch}: r = -0.13, RFI_{us}: r = -0.14). Non-esterified fatty acids were negatively correlated ($P \leq 0.05$) with ADG (heifer experiment, r = -0.22; steer experiment, r = -0.26), DMI (heifer experiment, r = -0.30; steer experiment, r = -0.45), RFI (heifer experiment, RFI_{Koch}: r = -0.28, RFI_{us}: r = -0.29; RFI_{size}: r = -0.30) and positively associated with G:F (steer experiment, r = 0.34). Glucose was negatively correlated ($P \leq 0.05$) with ADG (heifer experiment, r = -0.21) and G:F (heifer experiment, r = -0.17).

2.4. Discussion

In beef cattle production systems, animals with poor feed efficiency may represent a greater cost of production and may influence the environmental footprint of the livestock sector (Basarab et al., 2013). Therefore, identification and selection for cattle with improved feed efficiency is warranted and represents a relevant scope for improvements in both economical (Carstens, 2006) and environmental (Herrero et al., 2013) scenarios of livestock production. In the present study, the difference between efficiency groups observed in the RFI_{size} model represented up to 32 kg and 27 kg less DMI on a monthly basis for each feed efficient heifer and steer in comparison to their less efficient counterparts.

From a modelling perspective, it is important to note that the accuracy of RFI prediction models, can greatly vary between studies, with reported values ranging from 38 to 82% (Koch et al., 1963; Fitzsimmons et al., 2013; Freetly and Brown-Brandl, 2013; Mercadante et al., 2015). Thus, numerous attempts have been made to increase the prediction capacity of RFI while also ensuring biological differences are being accounted into the model proposed by Koch et al. (1963). For example, the inclusion of body composition traits (Basarab et al., 2003; Montanholi et al.,

2009) has been a successful addition to the previous Koch model. This addition may not only account for the difference regarding the differences in the energetic demand for fat and protein accretion (Owens et al., 1993), which may help verification of correlated responses to selection (Richardson and Herd, 2004), but also increased the accuracy of the prediction models (Montanholi et al., 2009). It was previously hypothesized that the addition of animal size traits, especially measurements of girth, to the RFI and RG models would represent an increase in the prediction capacity of these models, considering their potential to reflect internal organs demands (Kleiber, 1961) and its direct effects on DMI (NRC, 2016). To date, no attempts have been made in regards to the addition of body measurement traits in the prediction models of gain and intake. Our results demonstrated that the addition of girth measurements, across all experiments, increased the accuracy of prediction for both intake and gain models. This could be a valuable inexpensive addition to the sample collection routine and would potentially account for animal size variations and greater capacity for feed intake that are not being accounted for when using BW or metabolic BW in the prediction models. In fact, the metabolic weight ($BW^{0.75}$) proposed by Kleiber (1961) is an accurate factor to be used across species, but it might not accurately reflect the metabolic differences within each species that present smaller differences than the classic example of the elephant and the mouse (Schmidt-Nielsen, 1970). Furthermore, it has been shown that distinct metabolic states within species might require different exponents to properly calculate metabolic body weight (Labussière et al., 2016).

The absence of associations between RFI_{Koch}, RFI_{us} and RFI_{size} models, body and carcass composition traits, combined with the similarities in the different efficiency phenotypes are in agreement with previous studies (Arthur et al., 2003; Basarab et al., 2003; Montanholi et al., 2009) and might be suggestive that RFI has a weak association with body composition. To date, this is

still a controversy, since there are other studies that have reported differences in relation to protein and fat deposition among different efficiency groups (Richardson and Herd, 2004; Schenkel et al., 2003). Nonetheless, the addition of body composition traits in RFI prediction models is still valuable, since this might account for the differences in regards to energy needs for fat or protein deposition (Owens et al., 1993) to ensure carcass soundness at slaughter and reduce potential decrease in carcass quality. In the present study, the positive associations between DMI, ribeye area and G:F highlight the positive relationship between growth and gross efficiency measures (Archer et al., 1999) and reinforce and the concept that selecting for gross efficiency consequently results in larger animals, as reported previously (Crowley et al., 2010). The contrastingly negative association between DMI with intramuscular fat in heifers and the positive association between DMI and carcass marbling in steers could be attributed to a variety of different factors, such as diverse hormonal status, tissue accretion and age in relation to animals' growth curve (Garret, 1987; NRC, 2016) factors that were all different between the heifer and steer experiments in the current study. Animals' genotypes and genetic potential were additional sources of variation that were not accessed throughout the experiment. Thus, we believe the associations found in the steers could be attributed to the development of internal fat deposits (Andrews, 1958), which in finishing animals has been proven to increase with increased days on feed (Bruns et al., 2004) as well as dietary energy density and DMI.

Feeding patterns and activity could account for up to 12% of the variation in RFI (Richardson and Herd, 2004) and many studies indicate distinguished behavioral patterns across cattle with differing feed efficiency (Nkrumah et al., 2006; Nkrumah et al., 2007; Kelly et al., 2010; Montanholi et al., 2010). As expected, increased number of feeding events daily was positively associated with RFI, which has been shown elsewhere (Montanholi et al., 2010).

Furthermore, our findings illustrate the importance of feeding behavior traits and suggest their association not only with intake prediction models, but also with the gain prediction models as well as gross measurements of efficiency. Similar to Kelly et al. (2010), more efficient heifers in the present study visited the feeder less times daily. Noteworthy, the present study also suggests that more efficient heifers ate more (g of DM) during each visit. We attribute this result to the fact that, when summarizing the Insentec feeding data and calculating feeding behavior parameters, we included every feeding event with zero g of DM consumption, with intent to also access animal activity. Thus, we believe that the daily visits could be representative of animal activity and that more feed efficient heifers engaged in less daily feeding activity (Golden et al., 2008). Similarly, results showed that efficient steers exhibited diminished number of daily meals and visits, along with fewer amounts eaten per meal in comparison to their inefficient counterparts, which is in agreement with Montanholi et al. (2010).

Numerous attempts in determining the optimal animal size to achieve maximum biological and/or economic efficiency have been made (Johnson et al., 2010) due to their biological and economic impacts on animal production (Dickerson, 1978) and the potential of its variance to be used as an important resource for increasing production efficiency (Cartwright, 1979). Measurements of girth have been described to be positively associated with DMI, ADG, and feed conversion efficiency (i.e., F:G, the inverse measurement of G:F) in growing heifers (Kelly et al., 2010). The present results are in agreement with the previous findings, since all girth measurements exhibited moderate to strong positive correlations between girth measurements, DMI, ADG and G:F; and could be supported by the fact that greater animal size (i.e., BW) requires a greater DMI (NRC, 2016), and, consequently, daily gains and overall efficiency of gain in relation to feed will be greater considering the animals are larger. In agreement with Kelly et al.

(2010), the present study did not find any significant differences regarding animal size phenotypes between RFI groups.

Several metabolites and hormones have been associated with divergent feed efficiency phenotypes (Richardson et al., 2004; Gonano et al., 2014; Montanholi et al., 2017). The association between DMI and PUN found in the present study was expected and can be attributed to the close positive relationship of this metabolite with the level of intake (Lapierre and Lobley, 2001). In this context, the negative association between PUN and RFI also seems reasonable, since animals with low-RFI distinctly consume less feed. Additionally, there are also major metabolic expenses related to the process of urea recycling and clearance within the blood (Egan et al., 1984), which could also be influencing feed efficiency and may constitute one possible explanation for efficient animals to have lower maintenance requirements. However, the strength of this association is suggested to be fairly low (Kelly et al., 2010) and described not to have major effects on overall performance and efficiency (Richardson et al., 2004). Hence, lack of differences in relation to efficient phenotypes found in the present study (Figure 2.1A, 2.1D) reinforces this hypothesis and provides more indications that those associations may be mostly due to the positive association of dietary intake and urea (Clarke et al., 2009) rather than actual differences on efficiency of energy and protein use. The negative associations of plasma NEFA concentrations with ADG, DMI and RFI, along with the positive association with G:F have also been described elsewhere (Richardson et al., 2004; Kelly et al., 2010; Wood et al., 2014). Interestingly, feed efficient heifers had marked lower NEFA concentrations throughout the experiment, which is in accordance with previous studies (Kelly et al., 2010) and may be because of a potential higher nutrient delivery in efficient animals, since the circulation of NEFA serve as a reserve of readily available energy to peripheral tissues in growing animals (Drackley, 2005). The association between ADG and G:F with plasma

glucose along with the lack of associations with RFI or differences across divergent phenotypes found in the present study was also reported elsewhere (Richardson et al., 2004; Kelly et al., 2010). Altogether, this might be attributed to the fact that ruminants do not absorb high amounts of glucose from dietary intake or solely rely on glucose as a respiratory fuel (Weeks, 1979). Hence, lack of differences in relation to efficient animals provides more indications that glucose metabolism may not be of great relevance in explaining the biological variation of feed efficiency in growing animals.

In conclusion, linear measurements of girth seemed to be a valuable addition to the prediction models of gain and intake in growing animals. These measurements may be accounting for variation in animal size that are not reflected in BW or $BW^{0.75}$ and may represent a non-invasive inexpensive practice that could be easily applied into cattle handling routines. Body and carcass composition may be important players in the biological variation of feed efficiency and this relationship could be influenced by a multitude of factors (i.e., genotypes, hormonal status, tissue accretion and growth curve). Thus, the associations between body composition traits may vary across feed efficiency measures. It is interesting to note that behavioral patterns were associated with multiple measures of efficiency, and their respective associations indicated less daily activity in more efficient phenotypes. Animal size traits showed greater association with G:F and RG in comparison to RFI. Lastly, PUN, NEFA and glucose seemed to be highly dependent on DMI and ADG. However, only NEFA seemed to be associated with the efficiency measures of RFI and G:F.

The evaluation of different approaches for calculating RFI provided additional biological inferences about productive performance, feeding behavior, animal size and plasma metabolic markers. From all traits evaluated herein, the feeding behavior traits had the strongest relationship with the different estimates of RFI as calculated in these experiments. Based on this study, a more

feed efficient heifer visited the bunk fewer times a day but ate larger amounts at each visit, and had greater concentrations of NEFA in plasma; a more feed efficient steer also visited the bunk fewer times a day, and while having smaller meals, spent more time per meal and visit. These traits may represent important variation in the biological variation of efficiency of feed use and might be used as indirect assessments of efficiency.

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3. RELATIONSHIPS BETWEEN ANIMAL SIZE, FEEDING BEHAVIOR, PLASMA METABOLITES AND FEED EFFICIENCY IN BEEF CATTLE: II. MATURE PREGNANT COWS

3.1. Introduction

The provision of feed to animals is a major cost to beef production. This is especially relevant in the cow-calf herd, which may account for about 65 to 85% of overall feed costs (Montaño-Bermudez et al., 1990). It is unquestionable that adequate nutrition is needed for proper maintenance, growth and reproduction. However, there may be a large animal-to-animal variation in relation to how energy and nutrients are utilized (Richardson and Herd, 2004). This may enable the selection of more feed efficient breeding females, along with improvements in profitability and environmental impacts (Basarab et al., 2013) of beef production systems.

Several measures of feed efficiency have been proposed to assess efficiency of feed and energy use in beef cattle (Archer et al., 1999; Swanson and Miller, 2008). Traditional gross efficiency measurements (i. e. gain to feed ratio), residual gain and feed intake (Koch et al., 1963; Montanholi et al., 2009) have been intensively studied. However, even though the beef industry has been focusing on the topic of feed efficiency, most of these efforts have focused on growing animals (Berry and Pryce, 2014). In this context, another feed efficiency measure that might aid in the understanding of the biological variation of feed efficiency is cow/calf efficiency (Jenkins and Ferrell, 1994), which is expressed as the weight of the calf weaned (output) in relation to what has been consumed by the cow/calf unit (input) (Archer et al., 1999).

Several studies have been conducted to quantify the biological processes that might account for differences in feed efficiency. There is a great number of literature reviews on this topic (see: Richardson and Herd, 2004; Carstens, 2006; Montanholi, 2007; Arthur and Herd, 2008).

However, little effort have been made in the phenotypic characterization of mature feed efficient females. Recent studies have suggested the association between linear body measurements and blood metabolic markers with productive performance and efficiency measures (Wood et al., 2014), and differences in feeding behavior patterns (Xi et al., 2016).

We hypothesized that calving parameters, animal size, feeding behavior and plasma metabolic markers are associated with different measures of feed efficiency and may display differences in relation to efficient and inefficient phenotypes, measured through residual feed intake (RFI). Additionally, the adjustment of animal size measurements into prediction models of gain and intake may enable improvements on the accuracy of prediction models of feed efficiency. The objectives of this study were to: 1) evaluate the inclusion of animal size traits in feed efficiency prediction models of mature pregnant cows; 2) evaluate the association between calving parameters, animals size, feeding behavior, and plasma metabolites with different measures of feed efficiency; and 3) determine the differences in calving parameters, body measurements, feeding behavior, and plasma metabolites in animals diverging in feed efficiency measured through two different measurements of RFI.

3.2. Materials and methods

3.2.1. Animals, experimental conditions and dietary treatments

All procedures were approved by the North Dakota State University Animal Care and Use Committee. During the fall of 2015 and winter of 2016, a total of 46 multiparous, crossbred mature pregnant beef cows were part of a 135 day testing period and were housed at the Beef Cattle Research Complex (North Dakota State University, North Dakota State University, Fargo, United States). Cows were divided into groups of 11 or 12 animals per pen (15.24 m x 56.39 m) with free access to an outdoor yard, as well as an indoor feeding area equipped with 8 Insentec electronic

feeding stations (Hokofarm Group B. V., Marknesse, The Netherlands). Prior to the experiment, each cow received a radio frequency ID tag that was placed in the right ear and allowed for the recording of feed intake and behavioral assessments. A 21-day adaptation period occurred to provide animal acclimation to the research facility and the automated feeding system. Cows were fed a forage-based diet (Table 3.1), with two levels of corn supplementation (0 vs. 0.2% of BW), three times a day that allowed for *ad libitum* consumption (first feeding occurred at 0800 h, second at 1200 h and the last at 1600 h). The cows' dietary treatments are explained in detail by Tanner et al. (2017). Briefly, the control diet consisted of solely the forage-based TMR and the supplemented group received corn at 0.2% BW (chemical composition: 89.37% dry matter, 7.60% CP, 14.10% NDF, and 3.20% ADF) in addition to the forage-based TMR. For the first 43 days of experiment, the forage-based TMR (Diet 1, Table 3.1), on a DM basis, consisted of: 45.00% hay, 45.00% straw and 10.00% concentrated separated by-product. However, due to the loss of a cow from an impacted abomasum, the diet had to be reformulated (Diet 2, Table 3.2), and the ingredient composition of the forage-based TMR (DM basis) remained the same until the end of the testing period was: 60.00% hay, 30.00% straw and 10.00% concentrated separated by-product.

At the beginning and end of the feeding trial, a 2-day BW and measurements of animal size were taken. Performance evaluations that consisted of BW measurement and blood collection were performed on days 1, 78 and 135 of the experiment prior to feed delivery. These assessments were planned accordingly to the periods of mid- (day 110 of pregnancy) to late-gestation (day 188 of gestation), as well as closer to the calving date (day 245 of gestation).

Table 3.1. Ingredient and nutrient composition of TMR in pregnant cows.

Item (% DM)	Diet 1	Diet 2
Ingredient		
Hay	45.00	60.00
Straw	45.00	30.00
CSB[1]	10.00	10.00
Corn[2]		
Chemical composition		
DM	83.92	81.38
CP	6.40	7.10
NDF	67.00	64.50
ADF	42.30	38.90
Ca	0.28	0.37
P	0.12	0.26

[1]Concentrated separator by-product (partially de-sugared beet molasses).
[2]Supplemented cows received corn at 0.20% BW and control cows received no corn.

3.2.2. Feed analysis

Similar to Swanson et al. (2014), the diet samples were collected weekly. Samples were analyzed at the Nutrition Laboratory at North Dakota State University. Briefly, samples were dried in a 55°C oven and ground to pass a 1-mm screen. The samples were analyzed for DM, ash, nitrogen (N; Kjehldahl method), calcium, and phosphorus by standard procedures (AOAC, 1990) and for NDF (assayed with heat stable amylase and sodium sulfite and expressed inclusive of residual ash) and ADF (expressed inclusive of residual ash) concentration by the method of Robertson and Van Soest (1981) using a fiber analyzer (Ankom Technology Corp., Fairport, USA). Percent crude protein (CP) was calculated by multiplying N concentration × 6.25.

3.2.3. Productive performance and feed efficiency assessments

Individual feed intake was determined using the Insentec automated feeding system (Hokofarm Group B. V., Marknesse, The Netherlands). At the end of the experiment, feed intake

data was downloaded and used to calculate the average feed intake (DMI; kg) over the entire period. The feed intake data were filtered to exclude outlier records or days where mechanical problems potentially occurred, as previously described by Mader et al. (2009). Similar to Wood et al. (2014), pregnancy corrected average daily gain (pcADG, kg) was computed as the coefficient of linear regression of body weight on time of measurement, with the corrections of the uterus, fetal membranes and fetus (Silvey and Haydock, 1978). In addition, both DMI and pcADG were calculated as a percentage of mid-point pregnancy corrected BW (pcBW, kg; pcDMIrbw, pcADGrbw, %). The gain to feed ratio (G:F; ratio) was calculated as a ratio of ADG:DMI during the experiments' duration. The cow/calf efficiency index was also calculated. However, because cattle were moved to pasture before weaning, the calculations proposed by Jenkins and Ferrel (1994) were modified and was calculated based on cow intake during the test period until 3 weeks post calving (mid-gestation until calving) divided by the weight of the calf at 21 days of age (CCE_{d21}; kg of calf/kg DM). Both residual gain (RG), and residual feed intake (RFI) were modeled two different ways. The first (RG_{Koch} and RFI_{Koch}) were based on the models described by Koch et al. (1963), the second (RG_{size} and RFI_{size}) were based on the RFI models adjusted for gestation length (Wood et al., 2014) and animal size traits. All the RG and RFI models were calculated using the ordinary least squares (GLM procedure; SAS Institute Inc., Cary, USA), using mid-point pregnancy corrected $BW^{0.75}$, feed intake, gestation length and animal size measurements collected over the duration of the trial.

Overall, predicted gains were calculated as:

$$pcADG = \beta_0 + \beta_1(\text{mmpcBW; kg}) + \beta_2(\text{DMI; kg}) + \beta_{2+1}\ldots \beta_n(\text{days at pregnancy and animal size traits}) + \text{RG models } (RG_{Koch} \text{ or } RG_{size})$$

Where β_0 is the regression intercept, β_1 is the coefficient of regression for mid-point pregnancy corrected metabolic body weight, β_2 is the coefficient of regression for dry matter intake, $\beta_{2+1}\ldots\ \beta_n$ are the models' best fit the days at pregancy and animal size traits. RG_{Koch} and RG_{size} were the residue of this regression, and were used accordingly to each model. The selection criteria for each model across all experiments were based on the Bayesian information criterion (BIC) and R^2.

Overall, predicted intakes were calculated as:

$$DMI = \beta_0 + \beta_1(\text{mmpcBW; kg}) + \beta_2(\text{pcADG; kg}) + \beta_{2+1}\ldots\ \beta_n(\text{days at pregnancy and animal size traits}) + \text{RG models } (RFI_{Koch} \text{ or } RFI_{size})$$

Where β_0 is the regression intercept, β_1 is the coefficient of regression for mid-point pregnancy corrected metabolic body weight, β_2 is the coefficient of regression for pregnancy corrected average daily gain, $\beta_{2+1}\ldots\ \beta_n$ are the models' best fit the days at pregancy and animal size traits. RFI_{Koch} and RFI_{size} were the residues of this regression, and were used accordingly to each model. The selection criteria for each model across all experiments were based on the BIC and R^2.

3.2.4. Feeding behavior and animal size assessments

Feeding behavior traits were calculated similar to Swanson et al. (2014) and were summarized as: events (per day; number of bunk visits and meals), eating time (minutes; per visit, per meal, and per day), and eating rate (grams of DM; per visit and per meal). A visit was defined as each time the Insentec system detect an animal at a bunk, while a meal was defined as eating periods that might include short breaks separated by intervals not longer than 7 min (Forbes, 1995; Montanholi et al., 2010). The data were summarized as the average of each individual animal from the initial day until the last day of the experiment.

Body measurements were recorded similar to as described by Wood et al. (2014). Body length was defined as the distance from the point of shoulder to end of the rump, hip height was defined as the distance from ground to base of tail head and hip width the distance between the *crista iliaca*. For the girth measurements, heart girth was measured as the circumference around the midsection caudal to shoulder, mid-girth was measured as the circumference around middle over navel, and flank girth was measured as the circumference around the middle at the flank and cranially to the udder. Body length, girth measures and hip width were recorded using a fabric measuring tape, and hip height measurements were recorded with a livestock height measuring stick.

3.2.5. Plasma metabolic markers

Blood samples were be collected by jugular venipuncture while cows were restrained in the squeeze chute. Blood was collected using 1.1 x 25 mm blood collection needles (BD Vacutainer® Precision Glide, BD Inc., Franklin Lakes, USA) and 10 mL sodium heparin blood collection tubes (BD Vacutainer®, BD Inc., Franklin Lakes, USA). Immediately after collection, samples were kept at 4°C until centrifugation. The samples were centrifuged at 4 °C at 3000×g for 20 minutes. The plasma was decanted into three 2 mL micro centrifuge tubes and stored at -20°C until analysis. Urea concentration in plasma (PUN) was measured by the QuantiChrom™ Urea Assay Kit (BioAssay Systems, Hayward, USA) and was determined using the urease/Berthelot procedure (Chaney and Marbach, 1962; Fawcett and Scott, 1960). Non-esterified fatty acid (NEFA) concentration was analyzed using the acyl-CoA synthetase-acyl-CoA oxidase method using a kit from Wako Pure Chemical Industries (Dallas, TX). Glucose concentration was measured using the Infinity Glucose Hexokinase kit (Thermo Trace, Louisville, USA) and was analyzed using the hexokinase/gluxose-6-phosphate dehydrogenase method (Farrance, 1987). All

assays were performed using a 96-well microplate reader (Synergy, HI Microplate Reader, BioTek Instruments, Winooski, VT).

3.2.6. Statistical analysis

Individual cow was considered an independent variable and was evaluated as a random effect, RFI groups (high- and low-) in the two prediction models (RFI_{Koch} and RFI_{size}) and day were treated as fixed effects, and the interaction between day and RFI group was treated as a random effect. Productive performance along with calf performance, feeding behavior, animal size and plasma metabolic markers were the response variables evaluated. Statistical analysis was performed using the SAS® software (version 9.4; SAS Institute Inc., Cary, USA). Prior to statistical analysis, normality was tested and ensured through residuals' diagnostic plots using the general linear model of SAS. If needed, transformations were performed and values were back-transformed to be reported. A categorical analysis was carried out in order to compare the animals according to RFI values within each determination model (RFI_{Koch} and RFI_{size}). Means of the two RFI groups (high- and low-) in each of the models (RFI_{Koch} and RFI_{size}) for body and carcass composition, feeding behavior and animal size traits were tested using the general linear model of SAS, while the means for plasma metabolic markers were tested using the mixed procedure of SAS. The covariance structures used to test fit statistics of the mixed model included variance components, compound symmetry, autoregressive one, unstructured, and ante-dependence one. Smaller fit values (BIC) were always selected. The least square means comparisons for analysis conducted using both the general linear model and mixed model were performed using the Scheffé's test. The associations between calving parameters, feeding behavior, animal size and blood metabolites with productive performance traits were measured through partial correlations, adjusted for dietary treatment, using the MANOVA/PRINTE statement of the general linear

model. For all analyses, data were considered statistically significant when $P \leq 0.05$ and were considered a trend towards significance when $0.10 \geq P > 0.05$.

3.3. Results

3.3.1. Prediction models

The goodness of fit (R^2, CV, R MSE) for regression models of intake (RFI_{Koch}, RFI_{size}) and gain (RG_{Koch}, RG_{size}) can be found in Table 3.2. The addition of size traits in both prediction models ($RFI_{size,}$ RG_{size}) increased the accuracy of prediction by 12% for the models accounting for BW and BW gain (RFI_{Koch}) and 13% for the gain prediction model (RG_{size}).

Table 3.2. Model fit statistics for the selected residual feed intake (DMI models) and residual gain (ADG models) with differing covariates.

Experiment	Model covariates[†]	N	R^2	CV	R MSE
Cows	Residual feed intake				
	mpcmBW pcADG	45	0.26	7.93	1.15
	mpcmBW pcADG iHG iFG pregd	45	0.34	7.73	1.12
	Residual gain				
	mpcmBW pcADG	45	0.29	53.54	0.16
	mpcmBW pcADG iHG iFG pregd	45	0.42	50.31	0.15

[†] mpcmBW, mid-point pregnancy corrected BW; pcADG, pregnancy corrected ADG; pregd, days of pregnancy; iHG, heart girth; iFG, initial flank girth.

Table 3.3. Least square means of productive performance and calving parameters, measured in mature pregnant cows, by high- and low-RFI groups according to the two RFI determination models (RFI_{Koch} and RFI_{size}).

Traits (unit)	RFI_{Koch}			RFI_{size}		
	high-RFI[†]	low-RFI[†]	*P*	high-RFI[†]	low-RFI[†]	*P*
Productive Performance						
Initial pcBW (kg)	653 ± 10.73	660 ± 10.97	0.66	658 ± 10.99	655 ± 10.74	0.85
Final pcBW (kg)	694 ± 13.14	698 ± 13.43	0.87	700 ± 13.41	692 ± 13.11	0.70
pcADG (kg/d)	0.31 ± 0.04	0.29 ± 0.04	0.71	0.31 ± 0.04	0.28 ± 0.04	0.62
pcADG relative to BW (%)	0.04 ±0.005	0.04 ± 0.005	0.61	0.04 ± 0.005	0.04 ± 0.005	0.6
Dry matter intake (kg)	15.34 ± 0.20	13.57 ± 0.20	0.01	15.38 ± 0.20	13.62 ± 0.20	0.01
Dry matter intake relative to BW (%)	2.28 ± 0.03	2.01 ± 0.03	0.01	2.27 ± 0.03	2.03 ± 0.03	0.01
Gain to Feed (ratio)	0.02 ± 0.002	0.02 ± 0.003	0.81	0.02 ± 0.003	0.02 ± 0.002	0.91
Cow/Calf efficiency at d 21 (CCE_{d21}, kg of calf/kg DM)	0.22 ± 0.004	0.19 ± 0.004	0.01	0.22 ± 0.004	0.19 ± 0.004	0.01
RG (Koch et al. 1963) (RG_{Koch}, kg/d)	-0.02 ± 0.03	0.02 ± 0.03	0.43	-0.02 ± 0.03	0.02 ± 0.03	0.36
RG (size adjusted) (RG_{size}, kg/d)	-0.01 ± 0.03	0.02 ± 0.03	0.48	-0.01 ± 0.03	0.01 ± 0.03	0.52
RFI (Koch et al. 1963) (RFI_{Koch}, kg/d)	0.86 ± 0.14	-0.90 ± 0.15	0.01	0.85 ± 0.16	-0.82 ± 0.16	0.01
RFI (size adjusted) (RFI_{size}, kg/d)	0.77 ± 0.15	-0.80 ± 0.15	0.01	0.84 ± 0.14	-0.80 ± 0.14	0.01
Calving Parameters						
Gestation length (d)	278 ± 0.74	279 ± 0.76	0.66	279 ± 0.76	278 ± 0.75	0.79
Calf BW at birth (kg)	40 ± 0.71	41 ± 0.79	0.33	40 ± 0.79	41 ± 0.78	0.46
Calf BW at 21 d (kg)	70 ± 1.37	71 ± 1.47	0.52	69 ± 1.42	71 ± 1.39	0.27
Calf BW at 168 d (kg)	270 ± 4.52	270 ± 4.85	0.99	271 ± 4.73	270 ± 4.62	0.90

[†]Mean ± SEM.

RG = residual gain; RFI = residual feed intake

3.3.2. Productive performance and calving parameters

The RFI_{Koch} and RFI_{size} were different between the high- and low-RFI groups (Table 3.3). Feed inefficient cows (high-RFI) consumed 11% more feed daily over the feeding trial, this could represent 642 kg of extra feed per cow per year (Table 3.3). Notably, when comparing DMI as a percentage of BW, inefficient cows still consumed more feed than their efficient counterparts (Table 3.3). Interestingly, when considering the cow/calf efficiency index, inefficient cows produced more kg of calves per kg of DM consumed. However, calving parameters and gestation length did not differ between high- and low-RFI groups (Table 3.3).

The evaluation of the associations between productive performance with calving parameters revealed that both pcADG and pcADGrbw were negatively correlated ($P \leq 0.05$) with gestation length (r = -0.33; r = -0.34) and positively correlated ($P \leq 0.05$) with calf BW at day 21 (r = 0.35; r = 0.32) and calf BW at day 168 (r = 0.37; r = 0.35). The G:F ratio and RG_{Koch} were negatively correlated ($P \leq 0.05$) with gestation length (r = -0.34 and r = -0.42, respectively). Furthermore, G:F was also positively correlated ($P \leq 0.05$) with calf BW at 21 d (r = 0.34) and at 168 d (r = 0.35).

Table 3.4. Least square means of feeding behavior and animal size, measured in mature pregnant cows, by high- and low-RFI groups according to the two RFI determination models (RFI_{Koch} and RFI_{size}).

Traits (unit)	RFI_{Koch}			RFI_{size}		
	high-RFI†	low-RFI†	*P*	high-RFI†	low-RFI†	*P*
Feeding Behavior						
Meals (events/d)	48 ± 2.63	38 ± 2.69	0.01	46 ± 2.85	40 ± 2.80	0.17
Visits (events/d)	95 ± 4.96	75 ± 5.07	0.01	91 ± 5.37	80 ± 5.26	0.18
Daily time (min)	202.56 ± 7.33	195.29 ± 7.49	0.49	207.29 ± 7.32	191.09 ± 7.16	0.12
Time per meal (min/event)	4.64 ± 0.42	5.69 ± 0.43	0.08	5.10 ± 0.45	5.21 ± 0.44	0.86
Time per visit (min/event)	2.32 ± 0.21	2.83 ± 0.21	0.09	2.55 ± 0.22	2.60 ± 0.21	0.87
Eating rate per meal (g of DM/event)	347.01 ± 26.07	396.47 ± 26.66	0.19	368.95 ± 27.20	373.33 ± 26.60	0.91
Eating rate per visit (g of DM/event)	124.31 ± 7.78	89.85 ± 7.96	0.01	118.17 ± 8.50	97.22 ± 8.31	0.08
Animal Size						
Initial body length (cm)	107.62 ± 1.83	105.87 ± 1.87	0.51	107.78 ± 1.86	105.8 ± 1.82	0.45
Initial hip height (cm)	124.93 ± 0.84	128.84 ± 0.85	0.71	124.84 ± 0.84	128.76 ± 0.82	0.12
Initial hip width (cm)	59.03 ± 0.82	57.73 ± 0.84	0.28	59.69 ± 0.81	57.15 ± 0.79	0.03
Initial heart girth (cm)	197.73 ± 3.35	204.53 ± 3.42	0.16	203.43 ± 3.46	198.78 ± 3.39	0.34
Initial mid girth (cm)	244.34 ± 2.66	243.32 ± 2.72	0.79	243.21 ± 2.73	244.45 ± 2.67	0.75
Initial flank girth (cm)	210.82 ± 4.27	215.03 ± 4.32	0.49	216.30 ± 4.32	209.61 ± 4.23	0.27
Final body length (cm)	130.95 ± 1.07	128.5 ± 1.10	0.12	131.19 ± 1.08	128.38 ± 1.06	0.07
Final hip height (cm)	132.58 ± 2.32	133.02 ± 2.37	0.24	131.85 ± 2.37	133.69 ± 2.32	0.24
Final hip width (cm)	65.07 ± 5.11	57.5 ± 5.23	0.31	65.15 ± 0.53	57.76 ± 0.35	0.02
Final heart girth (cm)	199.47 ± 1.95	203.32 ± 2.00	0.17	201.24 ± 2.04	201.46 ± 2.00	0.93
Final mid girth (cm)	248.59 ± 2.73	248.68 ± 2.85	0.98	250.31 ± 2.77	246.96 ± 2.77	0.39
Final flank girth (cm)	213.25 ± 2.12	214.34 ± 2.18	0.72	214.14 ± 2.18	213.44 ± 2.13	0.82

†Mean ± SEM.

3.3.3. Feeding behavior

Less daily feeding events (meals and visits) and less amount of DM eaten per visit were observed in low-RFI_{Koch} cows ($P \leq 0.05$, Table 3.4). Additionally, it was also observed that efficient cows had up to 2-minute longer meals in comparison to their inefficient counterparts (Table 3.4). Furthermore, daily number of meals and visits were positively correlated ($P \leq 0.05$) with pcDMIrbw (r = 0.50 and r = 0.49, respectively), cow/calf efficiency (r = 0.42 and r = r = 0.42, respectively), and RFI_{Koch} (r = 0.40 and r = 0.40, respectively). Increased daily time spent at the bunk was correlated ($P \leq 0.05$) with increased pcADGrbw (r = 0.31) and increased RG (RG_{Koch}, r = 0.31; RG_{size}, r = 0.32). Furthermore, the amount eaten per visit (g of DM) was positively correlated ($P \leq 0.05$) with pcDMIrbw (r = 0.54), cow/calf efficiency (r = 0.48), RFI_{Koch} (r = 0.53) and RFI_{size} (r = 0.40).

3.3.4. Animal size

The RFI_{size} model suggested that efficient cows possessed smaller hip width ($P \leq 0.05$) and tended to have a shorter body length ($P \leq 0.10$; Table 3.4). Dry matter intake was the only trait that was correlated ($P \leq 0.05$) with linear measurements of body length (initial, r = 0.29; final, r = 0.32), initial hip width (r = 0.32) and final flank girth (r = 0.41).

3.3.5. Plasma metabolic markers

The results for plasma metabolic markers followed the same pattern across all RFI predictions. Therefore, the pattern of plasma metabolic markers across the entire testing period is being shown within the RFI_{size} estimate (Figure 3.1). There were no differences in PUN, NEFA or glucose between efficient and inefficient cows. Moderately strong negative correlations ($P \leq 0.05$) between NEFA and ADG (r = -0.49), DMI (r = -0.30), G:F (r = -0.48), cow/calf efficiency (r = -0.35), RG_{Koch} (r = -0.36) and RG_{size} (r = -0.32) were found.

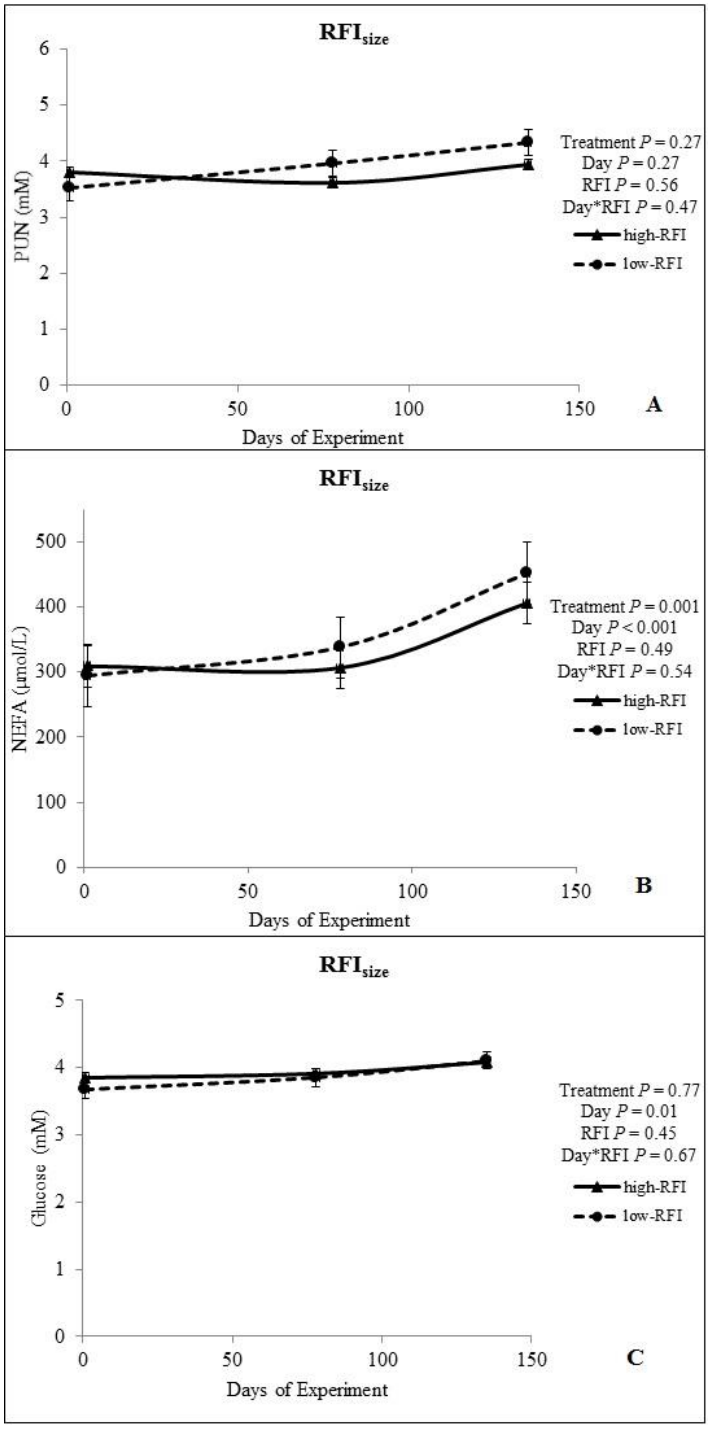

Figure 3.1. Plasma metabolites in mature pregnant cows over the performance evaluation (135 d) by feed efficiency group (RFI_{size} model, adjusted for size traits). (A) Plasma urea-N, (B) non-esterified fatty acids and (C) glucose.

3.4. Discussion

In comparison to accuracy of the growing animal prediction models presented and discussed in Chapter 2 and elsewhere (48 – 60%, Koch et al., 1953; 77%, Montanholi et al., 2009), the accuracy of prediction in mature animals (Table 3.2) was markedly lower in both intake (RFI_{Koch}, RFI_{size}) and gain (RG_{Koch}, RG_{size}) models. This has been shown in second parity pregnant heifers (Lawrence et al., 2011) and gestating mature beef cows (Lawrence et al., 2013; Wood et al., 2014). The present results regarding the RFI_{Koch} model displayed a similar R^2 range to the previous studies (24 – 29%, Lawrence et al., 2011, Lawrence et al., 2013; 21 – 54%, Wood et al., 2014). Despite the suggestions of increased variability when measuring RFI with high-forage diets (Meyer et al., 2008), we believe the lowered R^2 may reflect some of the challenges in measuring feed efficiency in mature cows because the output measures, such as body weight gain or loss, changes in body composition, or growth of the conceptus are difficult to quantify. Furthermore, during this period mature cows may also maintain body weight, having body weight gains close to zero (Morgan and Davis, 1936) or even lose weight (Fontoura et al., 2016). It is interesting to note, however, that similar to in growing animals (Chapter 2), the addition of size traits in the prediction models also increased the accuracy of prediction by up to 12% for RFI and 13% in RG models in mature pregnant cows. This may reinforce the addition of these traits to feed intake or ADG prediction models, as previously proposed in Chapter 2, but may also indicate improvements for the prediction models of mature animals.

The associations between increased pcADG, G:F and RG_{Koch} with decreased days at pregnancy, along with the associations between increased pcADG and G:F with greater calf BW seem reasonable because those factors are known parameters affecting gestation length (Knapp et al., 1940). The lack of associations between RFI predictions and calving parameters may indicate

a poor association between calving parameters with this measure of feed efficiency. Notably, the homogeneity of calving parameters when comparing efficient and inefficient cows was also found in cows divergently selected for RFI (Arthur et al., 2005) and pregnant heifers (Hafla et al., 2013). As expected, feed efficient cows (low-RFI) consumed less feed daily in both prediction models, as it has been described elsewhere (Wood et al., 2014). It is interesting to note that high-RFI cows also had higher cow/calf efficiency (or vice-versa), indicating that inefficient cows produced more 3 g of calf in relation to each kg of DM consumed, when compared to their efficient counterparts. However, the absence of differences in calf BW at birth, 21-d or 168-d among efficient and inefficient cows, may suggest that this difference might not be biologically relevant. Overall, calf performance uniformity found in the present study might be suggestive that selection for residual feed intake may not bring significant selection line differences for calving parameters (Crowley et al., 2011; Hafla et al., 2013). However, due to the lower number of animals in the present study, and the lack of studies focusing on this matter, further studies are warranted to verify this hypothesis and to ensure there is no collateral response to this selection.

Feed efficient cattle may display distinguished behavioral patterns in comparison to feed inefficient cattle. It has been demonstrated that efficient animals typically engage in less daily feeding activity (steers, Golden et al., 2008), eat smaller meals (steers, Montanholi et al., 2010) at a slower pace (Kelly et al., 2010), and visit the feeder less often (heifers, Kelly et al., 2010; steers, Montanholi et al., 2010) over the feeding test. Recent studies in mature females indicate that efficient cows spend less time in the bunk daily (Xi et al., 2016). This has also been reported in pregnant heifers (Hafla et al., 2013), which spent 26% less time at the bunk daily. In contrast, our results suggest that efficient cows visited bunks less and ate less meals daily, consumed 27% less feed per meal and tended to spend 21% more time in each of the feeding events. However, it is

interesting to note that the previous studies (Hafla et al., 2013; Xi et al., 2016) did not measure the time for each specific event. We attribute this discrepancy in the findings of feeding behavior patterns to different methodologies used to examine feeding behavior.

The positive associations between DMI, body length, hip width and flank girth presently found are in agreement with previous findings in mature pregnant cows (Wood et al., 2014), as well as growing animals (presented in Chapter 2). The lack of differences in animal body size according to RFI groups has also been reported in dairy cows (Xi et al., 2016). Thus, the lack of associations and differences between RFI phenotypes and animal size traits may be suggestive that no detrimental effects of increased cow size might be present in animals selected for improved RFI.

In the present study, no associations were found between the concentration of PUN and productive performance or differences between RFI groups. This is in contrast to the findings of Wood et al. (2014), who described positive associations between this metabolite and DMI, pcADG and RFI. However, as discussed in Chapter 2, the strength of this association is suggested to be fairly low (Kelly et al., 2010) and described not to have major associations with overall performance and efficiency (Richardson et al., 2004). The negative correlations of NEFA with pcADG, DMI, G:F, cow/calf efficiency and RG are in agreement with previous findings in growing heifers (Chapter 2; Kelly et al., 2010), steers (Chapter 2; Richardson et al., 2004) and mature pregnant cows (Wood et al., 2014). This could indicate that, regardless of stage of production, fat metabolism might play an important role in the variation of feed efficiency (Wood et al., 2014; Gonano et al., 2014). However, in the present study, no differences in NEFA patterns between the efficiency groups were found. This is opposite to the findings of Xi et al. (2016), who found markedly lower NEFA concentrations in more feed efficient dairy cows. The lack of

associations between glucose and feed efficiency (measured through RFI) was also found in mature cows (Wood et al., 2014; Walker et al., 2015; Xi et al., 2016) and may be suggestive that, even though glucose is the primary source of energy for the conceptus (Bell and Bauman, 1997), differences in glucose metabolism between animals may not play an important role in the regulation of feed efficiency as it has been suggested elsewhere (Richardson et al., 2004; Kelly et al., 2010).

Overall, linear measurements of girth seemed to be a valuable addition to the prediction models of gain and intake in mature females. These measurements may be accounting for variations in animal size that are not reflected in BW or $BW^{0.75}$ and may represent a non-invasive inexpensive practice that could be easily applied into cattle handling routines. Gestation length, calf BW at birth, at day 21 and at day 168 of life did not differ across divergent RFI grouping in both RFI predictions (RFI_{Koch}, RFI_{size}). It is interesting to note that behavioral patterns were associated with multiple measures of efficiency, and in mature cows, their respective associations may differ depending on the efficiency measure used. Animal size traits in the mature cow may have a closer association with eating capacity (i.e., DMI) than with feed efficiency measures. Lastly, the three metabolic markers evaluated in the present study were not strongly associated with productive performance or feed efficiency measures in mature cows.

The evaluation of different models of RFI provided additional biological inferences about productive performance, calving parameters, feeding behavior, animal size and blood metabolic markers. In essence, more efficient cows had less daily intake with no differences in gestation length, calf body weight at birth and at weaning. However, the cow/calf efficiency index (CCE_{d21}) seemed to be reduced for efficient animals (low-RFI), which may be suggesting lighter calves from low-RFI animals at day 21 of age. From all traits evaluated herein, feeding behavior was the

category that presented more differences in relation to efficiency phenotypes based on RFI classification. Based on this study, a more feed efficient cow consumed fewer meals daily, visited the bunk less times a day and ate less at each visit, but tended to stay 21% longer in each feeding event (meals and visits). These results may provide further information on the basic aspects contributing to differences in feed efficiency in mature cows and reinforce the importance of feeding behavior and animal activity in the context of feed efficiency. Considering the present findings, future studies are warranted to verify the associations between RFI and the cow/calf efficiency index. The traits evaluated in the present study indicate that the biological variation of efficiency of feed use in growing animals (Chapter 2) and mature animals might differ.

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4. SUMMARY AND CONCLUSIONS

There are several economic and environmental benefits associated with the improvement in the efficiency of feed utilization. However, the complexity of feed efficiency, which is influenced by several traits and can be assessed through a myriad of different measures, impose several implementation obstacles by the industry. To date, there is still much controversy in regards of what is the biological basis of feed efficiency. This is not only important for research focused on the development of new proxies for feed efficiency, but also to ensure the lack of collateral response to genetic selection of animals with improved feed efficiency. The studies conducted and presented in this thesis have allowed for the opportunity to evaluate the association between important traits in beef cattle such as body composition, feeding behavior, animal size and plasma metabolites across different measures of feed efficiency and at different stages of beef cattle production.

The experiments presented in Chapter 2 and Chapter 3 demonstrated that the addition of linear measurements of girth seemed to be a valuable addition to the prediction models of gain (RG_{Koch}, RG_{us}, RG_{size}) and intake (RFI_{Koch}, RFI_{us}, RFI_{size}) in beef cattle, with improvements in accuracy ranging between 1 to 13%. These measurements may not only represent a non-invasive and inexpensive practice that could be easily applied into cattle handling routines at performance experiments, but also may be accounting for variations in animal size that are not reflected in body weight or metabolic body weight measures.

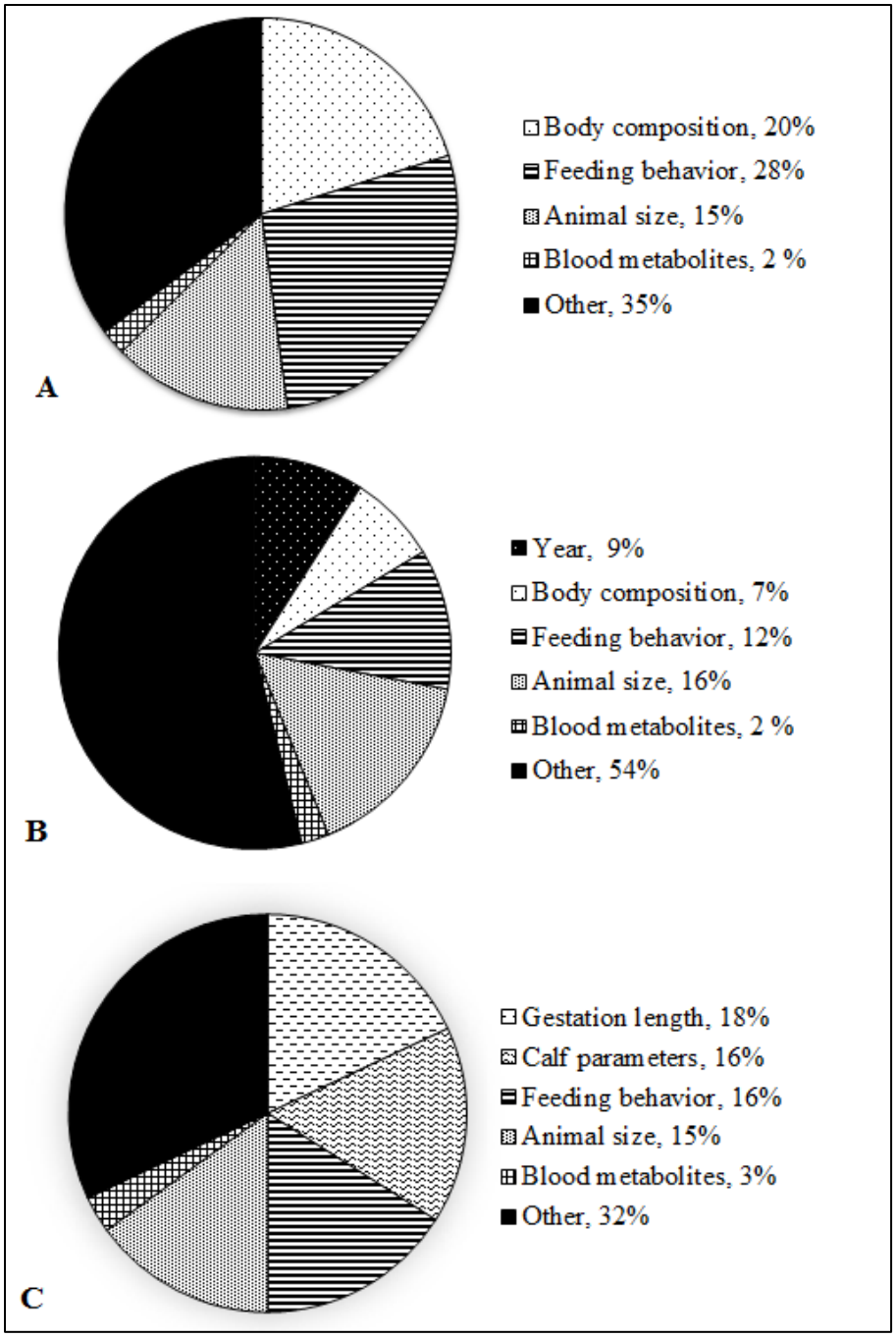

Figure 4.1. Contributions of body composition, feeding behavior, animal size and blood metabolites traits to the explained variation in gain to feed (G:F) in (A) steers, (B) heifers (with the addition of year), and (C) cows (with the addition of gestation length and calf parameters).

In general, body composition, feeding behavior, animal size and plasma metabolites were associated with the different measures of feed efficiency. However, the extent of this association was variable across animal stage and feed efficiency measure (G:F, RG, or RFI). To illustrate these differences, partial regression analyses were performed using the SAS software (version 9.4; SAS Institute Inc., Cary, USA), to summarize the overall contributions of body composition, feeding behavior, animal size and plasma metabolites traits to the explained variation in the different measures of efficiency. Figure 4.1 illustrates the contribution of these traits to G:F. In steers, feeding behavior, body composition and animal size accounted for most of the variability of this measure, whereas in heifers, animal size and feeding behavior were the most relevant traits. It was interesting to note that all traits evaluated were highly relevant in pregnant cows, with gestation length, calf parameters and feeding behavior accounting for at least 50% of the G:F variation.

Residual gain was the feed efficiency measure with the least percentage of variation explained by the traits studied herein (Figure 4.2). However, regardless of experiment, the largest contributions for this efficiency measure were animal size and feeding behavior traits, which represented 24%, 21% and 36% in the known variation of residual gain in steers, heifers and cows, respectively. Residual feed intake was the feed efficiency measure with the highest percentage of variation explained by feeding behavior (Figure 4.3). With the exception of the steer experiment, animal size showed little importance in the variation of RFI, when compared to the G:F and RG efficiency measures.

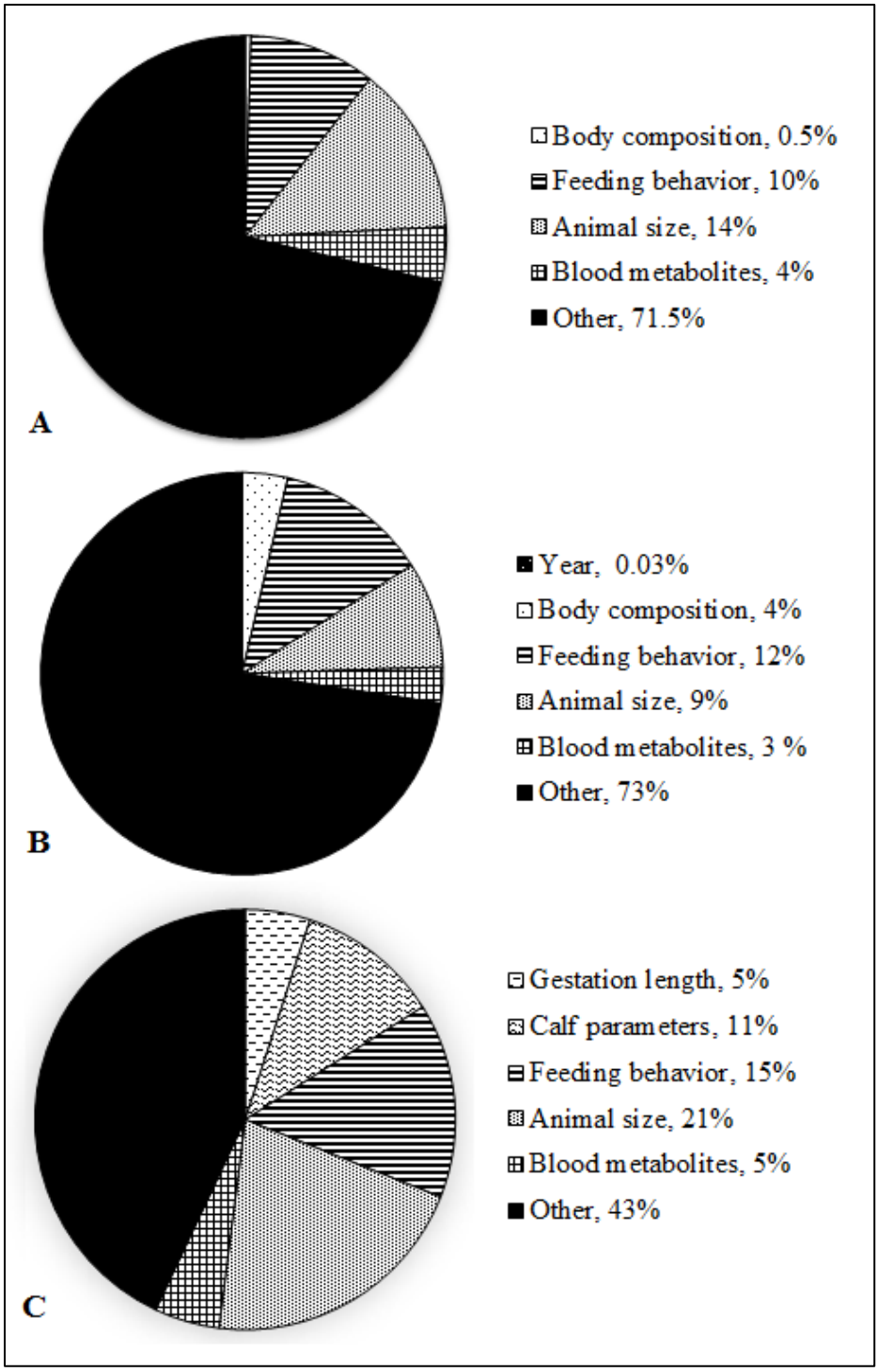

Figure 4.2. Contributions of body composition, feeding behavior, animal size and blood metabolites traits to the explained variation in residual gain (RG_{size} model) in (A) steers, (B) heifers (with the addition of year), and (C) cows (with the addition of gestation length and calf parameters).

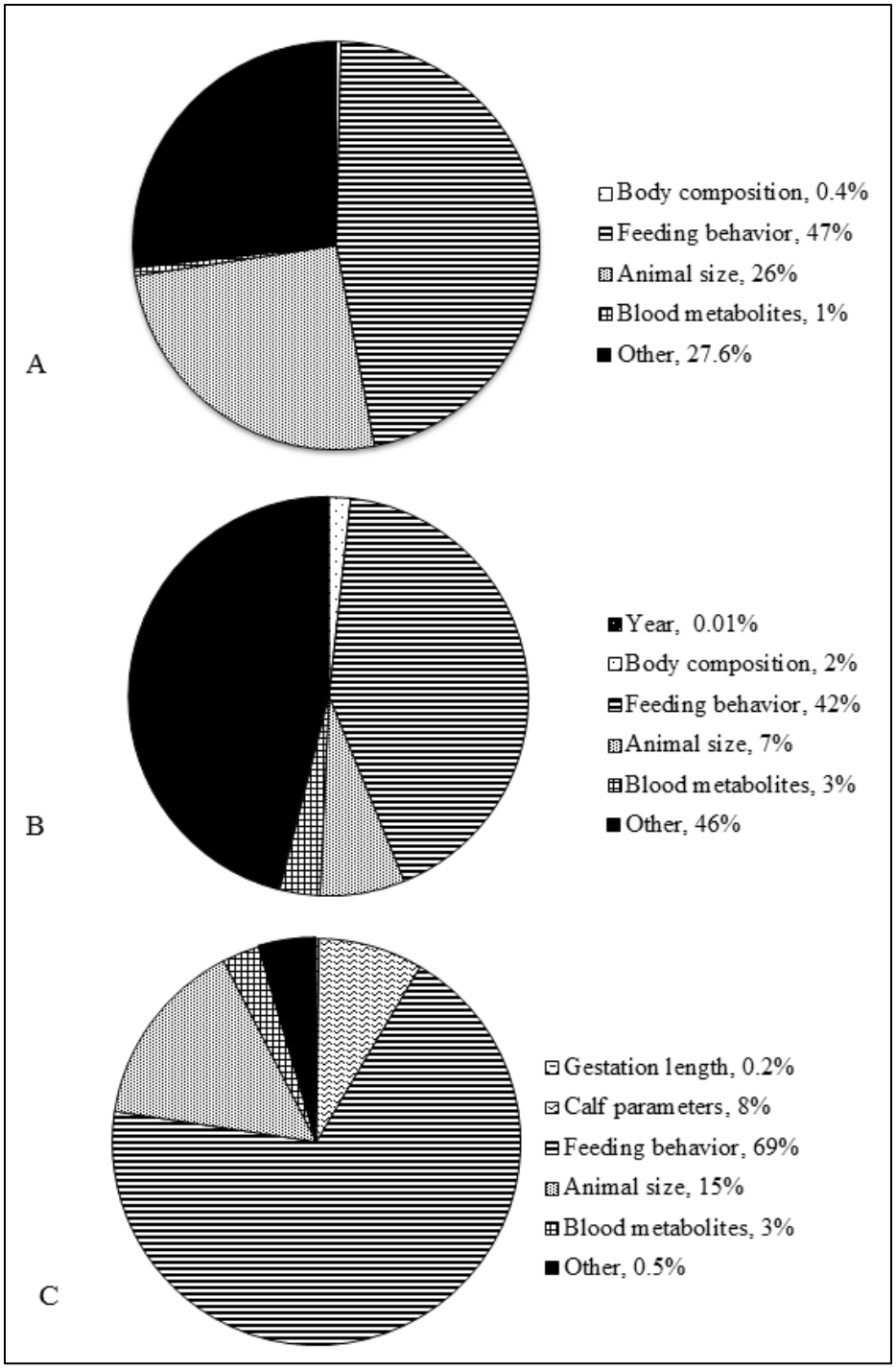

Figure 4.3. Contributions of body composition, feeding behavior, animal size and blood metabolites traits to the explained variation in residual feed intake (RFI_{size} model) in (A) steers, (B) heifers (with the addition of year), and (C) cows (with the addition of gestation length and calf parameters).

The analysis of the different RFI models (RFI_{Koch}, RFI_{us}, RFI_{size}) provided important information regarding differences between efficient (low-RFI) and inefficient (high-RFI) phenotypes. Among all categories of traits evaluated, feeding behavior differed the most in relation to efficiency phenotypes. Based on the findings of Chapter 2 and 3, feed efficient (low-RFI) heifers, steers and cows visited the bunk fewer times a day, which may be indicating reduced activity in efficient phenotypes, regardless of stage. However, differences were found in relation to meal size and time across experiments. While feed efficient heifers ate more (g of DM) each visit, efficient steers and cows ate less in each meal and visit but stayed longer in each feeding event. Body composition, animal size and calving parameters and blood metabolite traits did not seem to be affected by RFI classification. Furthermore, the similarity in NEFA, productive performance and feed efficiency correlations across stages of production suggests that efficient phenotypes possess higher concentration of this metabolite. However, the robustness of this correlation may not be sufficient for this metabolite to become a single marker to predict feed efficiency. Notably, heifers were the only category to express this difference in the least square means analysis.

In summary, linear body measurements seemed to be a valuable addition to prediction models of gain and intake. Animal size traits seemed to be more relevant to the measures of G:F and RG, rather than RFI. However, this association tended to vary across stage of production. Feeding behavior may constitute an important physiological factor regulating feed efficiency across efficiency measures and shows potential to be used for the development of new proxies of feed efficiency in the future. The diminished number of associations between plasma metabolites and feed efficiency suggest that these metabolites (PUN, NEFA and glucose) play minor roles in the variation in feed efficiency in beef cattle. It is notable that outputs of interest differ accordingly

to each stage of beef cattle production. Based on the present findings, G:F ratio and RG may be good indicators of efficiency in animal stages that are not impaired by an increase in animal size and growth (i.e. finishing animals) in comparison to the potential detrimental effects on the breeding herd (increased cow size and nutritional requirements). Overall, RFI seemed to be a good indicator of feed efficiency in growing animals. However, future studies involving a larger population of mature cows along with longevity assessments are warranted to further investigate the presently found associations between RFI and the cow/calf efficiency index. Regardless of efficiency measure, production systems that base selection criteria on efficiency of feed utilization should take into account animals' stage of production and system's outputs of interest.